Ann. Natal Mus. Vol. 33(2) Pages 379–459 Pietermaritzburg October, 1992

Revision of the Umboniinae in southern Africa and Mozambique (Mollusca: Prosobranchia: Trochidae)

by

D. G. Herbert
(Natal Museum, P. Bag 9070, Pietermaritzburg, South Africa)

ABSTRACT

All species of the Umboniinae known to occur in the seas off southern Africa and Mozambique are discussed (12 species, 4 new, belonging to 4 genera, 2 new). Observations on the external anatomy, radula and behaviour are given whenever possible. The systematics of the subfamily as a whole are discussed in the light of new data presented. The subfamily contains species with a monopectinate ctenidium and species with a bipectinate ctenidium. Several genera exhibit a morphology intermediate between more typical trochids and the highly derived members of the Umboniinae. The genus *Lirularia* is considered to be umboniine. Type specimens of a number of extralimital species are illustrated.

New genera: *Inkaba*, type species *Inkaba tonga* sp. n.; *Pseudominolia*, type species *Solariella splendens* Sowerby, 1897.

New species: *Ethalia bysma*, *E. electra*, *E. gilchristae*, *Inkaba tonga*.

New synonyms: *Minolia variegata* Odhner, 1919 = *Pseudominolia splendens* (Sowerby, 1897); *Margarita dilecta* A. Adams, 1855 = *Antisolarium egenum* (Gould, 1849); *Minolia eucoronata* Sowerby, 1905 = *Ethminolia impressa* (G. & H. Nevill, 1869).

New combinations: *Solariella splendens* Sowerby, 1897, and *Margarita articulata* Gould, 1861, belong to *Pseudominolia* gen. n.; *Solarium impressum* G. & H. Nevill, 1869, *Solariella sculpta* Sowerby, 1897, *Cyclostrema gravieri* Lamy, 1909, and *Solariella durbanensis* Kilburn, 1977, belong to *Ethminolia* Iredale, 1924.

New records: *Ethalia carneolata* Melvill, 1897, *Ethminolia nektonica* (Okutani, 1961) and *Ethminolia stearnsii* (Pilsbry, 1895) are recorded for the first time from the south-western Indian Ocean; *Ethminolia durbanensis* (Kilburn, 1977), *E. gravieri* (Lamy, 1909), *E. sculpta* (Sowerby, 1897) and *Pseudominolia splendens* (Sowerby, 1897) are recorded from Mozambique for the first time.

Lectotypes designated and figured: *Ethalia carneolata* var. *rubrostrigata* Melvill, 1904; *Ethalia minolina* var. *infralaevior* Schepman, 1907; *Ethalia striolata* A. Adams, 1855; *Margarita dilecta* A. Adams, 1855; *Minolia eucoronata* Sowerby, 1905; *Minolia glaphyrella* Melvill & Standen, 1895; *Minolia stearnsii* Pilsbry, 1895; *Minolia variegata* Odhner, 1919; *Monilea philippii* A. Adams, 1855; *Solariella splendens* Sowerby, 1897; *Solarium impressum* G. & H. Nevill, 1869.

Types figured: Holotype – *Cyclostrema gravieri* Lamy, 1909; syntype – *Ethalia carneolata* Melvill, 1897; holotype – *Ethalia minolina* Melvill, 1897; holotype – *Margarita articulata* Gould, 1861; holotype – *Minolia edithae* Melvill, 1891; holotype – *Monilea vernicosa* Gould, 1861; holotype – *Solariella durbanensis* Kilburn, 1977; lectotype – *Solariella sculpta* Sowerby 1897; holotype – *Solarium egenum* Gould, 1849; holotype – *Talopena gloriola* Iredale, 1929; syntype – *Trochus eudeli* Deshayes, 1863; holotype – *Trochus (Solariella) lamprus* Watson, 1880.

INTRODUCTION

The Umboniinae is a group of small trochids exhibiting several synapomorphic characters by which they can be relatively easily recognised. The shell is generally rather depressed, often glossy, the columella frequently with callus deposit, the protoconch beaked, and the surface frequently sculptured by microscopic, scratch-like, axial lines. Conchological characters, however, may not be entirely

diagnostic; more important are features of the radula and external anatomy. These are discussed further below.

There has been no previous revision of the southern African Umboniinae and the few existing records for this area are scattered though the literature. Barnard (1963) dealt with only three species. Until recently the amount of umboniine material available from southern Africa was limited and in many cases was inadequate for meaningful study. Dredging undertaken on the continental shelf off Zululand during 1987–90, however, has greatly increased the Natal Museum's holdings of most species, a number of which were not previously known to science. The need for a revision of the local Umboniinae became evident whilst studying the southern African Solariellinae (Herbert 1987). The two subfamilies have been much confused in the past, largely as a result of inadequate definitions. Several supposedly solarielline taxa examined during the course of my studies evinced umboniine affinities, demonstrating the need for a thorough examination of both subfamilies. I drew attention to this in my revision of the Solariellinae and highlighted the characters which may be used to separate members of the two subfamilies. When examination of the radula and external anatomy is possible the two are easily distinguished. In most cases, given a little experience, an accurate assessment can be made using the shell alone, particularly if the protoconch is in good condition.

MATERIALS AND METHODS

The bulk of the material discussed in this work was obtained during dredging cruises undertaken by staff of the Natal Museum off south-eastern Africa (NMDP). Sampling concentrated on the Zululand continental shelf was the most productive. Littoral material was obtained from a variety of sources, the most important of which was that collected in Durban Bay, by Henry Burnup at the turn of the century and more recently by Bernard Young from reclamation sand dredged in shallow water. Mozambican material has been accumulated over many years, largely by Eva Roscoe, Kurt Grosch and Richard Kilburn.

Type specimens of a number of species held in the AMSA, ANSP, BMNH, MCSN, MNHN, NMWC, NHMW, NHRS, USNM and ZMAN have been examined together with a range of comparative material (primarily type species) from the AMSA, MNHN, MVMA, NMNZ, SAMC, SAMA and ZMUC. Thiele's *Valdivia* type material, housed at the ZMHB was not available for study.

In the following descriptions shell coloration, where possible, is given according to the ISCC-NBS 1965 colour charts. In many cases, however, shell colour is so variable, both between and within individuals, that these charts are of little practical use. Coloration is rarely of value as a taxonomic character in this group and in most cases only an indication of the range of colour variation and patterning is given. Coloration is mentioned in the diagnoses only when it is of significance and then in more subjective terms for the benefit of those without access to the charts.

Protoconch diameter was measured according to the method set out previously (Herbert 1987). Radulae were dissected out, macerated in dilute NaOH,

sonicated briefly, air-dried via alcohol and mounted on stubs using double-sided tape. Gold-coated specimens were then examined at low accelerating voltage (5 Kv) in a Jeol T/200 or Hitachi S-570 scanning electron microscope.

MORPHOLOGY

Protoconch

All local members of the Umboniinae possess a small protoconch (diameter <250 μm, usually 180–200 μm), of more or less similar morphology. Typically it consists of just over one whorl, as in most trochids, and generally possesses a sinuous terminal lip and a pronounced apical beak. The beak is particularly well developed in genera such as *Ethminolia* (Fig. 58), *Pseudominolia* gen. n. (Fig. 87) and *Vanitrochus* (Herbert 1989) and often fuses with the terminal lip. It is perhaps least developed in *Ethalia,* where instead an inward extension of the terminal lip appears to join the otherwise rounded protoconch apex (Fig. 19). In some taxa the protoconch shows little superficial sculpture (eg. local species of *Ethalia*), but several species belonging to *Ethminolia*, *Inkaba* and *Pseudominolia* have an almost honeycomb-like surface reticulation (Figs 49, 54, 58). To some extent this resembles the characteristic sculpture of the protoconch in the Calliostomatinae and Thysanodontinae, but the similarity is probably homoplasious. In the Umboniinae this sculpture is far less regular and well defined than that in the other two subfamilies (Bandel 1982, Marshall 1988, Ramón 1990), and tends to become spirally aligned towards the protoconch aperture. *Lirularia* Dall, 1909, also has a small, strongly beaked protoconch with a somewhat honeycomb-like superficial reticulation (Hadfield & Strathmann 1990).

The possession of a small, beaked protoconch may, in some instances, be a useful taxonomic character and can serve to distinguish members of the Umboniinae from subfamilies such as the Solariellinae, which may otherwise have a similar shell morphology (Herbert 1987). The presence of a beak on the protoconch, however, is not unique to the Umboniinae and occurs, amongst other subfamilies, in the Margaritinae and Trochinae (Fretter & Graham 1977). Whether this represents a primitive character or a derived one which has been independently acquired on several occasions is not clear. Its functional significance to the developing larva, other than perhaps to provide increased strength, is not known.

The paucispiral nature of the protoconch is typical of the Trochidae and almost certainly indicates a lecithotrophic mode of development. It might also be suggested that its small size reflects indirect development with a planktonic dispersal stage. However, Hadfield & Strathmann (1990) have shown that species with a small protoconch may undergo either direct (benthic) or indirect (planktonic) development and that reliable predictions regarding developmental modes cannot be made on the basis of protoconch morphology in archaeogastropods. In fact their observations indicate that protoconch form may have greater phylogenetic significance than many modern workers have been prepared to accept.

Radula

Radulae of a number of umboniine taxa have been figured in the literature

(Thiele 1891 1924, Schepman 1908, Taki 1929, Powell 1930, Kuroda & Habe 1954, Barnard 1963, Yaron 1978, Hickman 1980 1984 1985, Hickman & McLean 1990). The formula is generally $\infty + (1) + 5 + 1 + 5 + (1) + \infty$, though there may be some variation in the number of laterals; Powell (1930) illustrated only four laterals in *Antisolarium egenum* (Gould, 1849) and *Zethalia zelandica* (Hombron & Jacquinot, 1854), whilst Taki (1929) figured six laterals in *Umbonium costatum* (Valenciennes in Kiener, 1838–9).

The umboniine radula is characterised by the reduction and more often absence of shafts and cusps on the rachidian and laterals. The central field of the radula ribbon thus bears only tooth base plates, and these too may be reduced to thin chitinous vestiges or even absent (Hickman 1984 1985). The marginals are numerous and well developed and are clearly the major food-gathering teeth. In light-microscope mounts the densely staining marginals often overlie and obscure the more weakly stained outer laterals making these difficult to see. This may account for some of the apparent variability in the number of lateral teeth. In most, if not all, genera there is a modified tooth, the latero-marginal plate, between the outer lateral and the marginals. This plate, if counted as a lateral, may further contribute to the apparent variability in the number of laterals. The shape of the plate varies between genera, but in most cases it retains a small shaft and cusp (Fig. 32). The inner marginal teeth have strongly recurved cusps which in the less specialised genera are spatulate with a well developed secondary cusp basally and few lateral serrations. Marginal cusps of this shape are present in a number of trochine genera and this is probably the plesiomorphic condition. Genera such as *Inkaba* and *Pseudominolia* which show greater anatomical specialisation have marginal teeth with shorter, broader cusps, each with a number of lateral denticulations. Whether or not this is indicative of a trend throughout the more advanced umboniines remains to be investigated. The food groove beneath the cusps of the marginals is simple in all local genera, but is exaggerated in some extralimital ones, for example *Antisolarium*, by the presence of a triangular expansion of the tooth shaft beneath the recurved cusp (personal observation).

The reduction in development of the radula has been linked to the filter-feeding habit shown by certain genera (eg. *Umbonium*), but there are several problematic inconsistencies with this idea. Firstly, genera such as *Ethalia* and *Monilea*, which lack any anatomical specialisations for filter-feeding and probably represent an early stage in the evolution of the subfamily, already show considerable reduction of tooth cusps in the central radula field. Secondly, as pointed out by Hickman (1985), facultative filter-feeders such as *'Minolia' biangulosa* (A. Adams, 1855) may have more reduced radula teeth than more or less obligate filter-feeders such as *Umbonium vestiarium* (Linnaeus, 1758). It seems more probable that the reduction of tooth cusps has little to do with filter-feeding and is an apomorphy developed in ancestral forms for other reasons, possibly in response to a non-selective deposit-feeding existence on soft substrata, prior to the evolution of filter-feeding within the subfamily. Filter-feeding mesogastropods (including members of the superfamilies Cerithioidea, Stromboidea, Vanikoroidea, Calyptraeoidea and Vermetoidea) show no significant trend toward the reduction of

tooth cusps (Bandel 1984). In these groups similarities and differences in radula form are more reflective of phylogenetic relationships than of mode of feeding.

One aspect of radula reduction which may well be correlated with the filter-feeding mode of life is the total length of the structure (number of transverse rows of teeth) and the size of the odontophore and snout. Genera with a bipectinate ctenidium (tribe Monileini) and which almost certainly feed entirely by deposit-feeding, have a radula of *ca* 70 to 80 transverse rows, a relatively well muscularised odontophore and a wide forehead and well developed snout. In contrast, genera with a monopectinate ctenidium (tribe Umboniini), which may supplement deposit-feeding, to a greater or lesser extent, with filter-feeding, have a shorter radula (35–45 rows in *Pseudominolia*) frequently with a much reduced odontophore and snout (Fretter 1975 and personal observation). Filter-feeding mesogastropods appear to exhibit a similar correlation (Thiele 1929, Graham 1938, Fretter & Graham 1981, Bandel 1984, Beck 1991).

Operculum

Hickman & McLean (1990) summarised opercular structure within the Trochoidea, but little detailed comparative information is available. In the Umboniinae the operculum is a well developed, relatively thick, circular disc which completely closes the aperture when the animal withdraws. It is typical of that of the Trochidae in being of the noncalcified multispiral planorboid type (cf. Taki 1950), but the number of whorls is smaller (less than ten in all species examined) than in some of the better known trochid genera such as *Gibbula* and *Calliostoma* (Fretter & Graham 1962, Gonzalez, Rato & Fernandez 1983), and the growing edge longer than is perhaps usual for the family (Hickman & McLean 1990). Peripherally there is a thin, frequently radially striate fringe which folds outward as the operculum is withdrawn into the aperture, forming a seal against the peristome. The width of this fringe varies interspecifically.

In most Umboniinae examined the operculum is transparent and its outer surface is smooth and glossy, marked only by growth-lines. However, in the two species here placed in the new genus *Pseudominolia*, the operculum is at most translucent and its outer surface appears lustreless due to the presence of numerous very fine and close-set concentric (spiral) lirae. This is a potentially useful taxonomic character which has not been identified previously and which merits further study. Insufficient data are available to draw any further conclusions at present.

Anatomy

The only extensive study of umboniine anatomy published to date is that of Fretter (1975), on the filter-feeding species *Umbonium vestiarium*. Brief descriptions and figures of the external features of other species have been given by Taki (1929), Okutani (1958 1961), Gofas, Afonso & Brandão (1986), McLean (1986) and Kase (1989), whilst Hickman (1985) compared *U. vestiarium* with a further two species from Hong Kong. A synopsis combining all existing information regarding external anatomy with many new observations was given by Hickman & McLean (1990) in their suprageneric revision.

The majority of southern African species have been obtained alive and I have been able to make observations on their external anatomy. The following general comments on the group are based on these observations and those mentioned above.

Members of the Umboniinae possess many typically trochoidean anatomical features such as epipodial tentacles and sense organs, and well developed neck lobes. In addition they exhibit several ostensibly apomorphous features which, when taken in conjunction with the radula and protoconch, characterise the group with reasonable precision. The majority of these features probably represent adaptations towards life in and on soft substrata, and some are clearly linked with filter-feeding.

Distinctive features of the cephalic region include papillation of the snout, reduction in the size of the snout, long mobile eye stalks which curve upwards and extend well beyond the edge of the shell during life, a narrow intertentacular region (forehead) with no lappets, and loss of the right post-optic tentacle. The neck lobes are well developed. The right lobe is evidently similar in shape throughout the subfamily, has a simple margin and forms a tubular exhalant siphon. The left neck lobe, in contrast, varies greatly in form within the subfamily; at its simplest, it comprises a low fold with close-set, unbranched, digitate projections (eg. *Ethalia*), whilst in the filter-feeding *Umbonium* it is greatly hypertrophied and forms a complex inhalant siphon and coarse filter (Fretter 1975). There are also several intermediary states with branching tentacular processes. The epipodium continues posterior to the neck lobes and bears a series of tentacles (usually four) with associated sense organs. The foot is broad anteriorly, tapers to a point posteriorly and has a bifid propodium which plays an integral part in locomotion and burrowing.

Fretter (1975) noted that the ctenidium of *U. vestiarium* extends the whole length of the mantle cavity, is monopectinate and is attached to the mantle skirt throughout its length. Hickman & McLean (1990) stated that the ctenidium is monopectinate in all members of the Umboniinae and noted further that the ctenidial filaments are elongate, possess swollen tips and have prominent bursicles. This is certainly true of most umboniine genera, but as will be discussed later it is not, in fact, true for all. The less specialised genera, here treated as the tribe Monileini, retain a bipectinate ctenidium in which the tip is free and the afferent ctenidial membrane long, extending well beyond the junction of the transverse pallial vein and the afferent branchial vessel, ie. similar to that of the Trochinae, Stomatellinae, Calliostomatinae and some Solariellinae. Even in the Monileini, however, the individual ctenidial filaments are elongate rather than triangular, and have swollen tips and distinct bursicles. Whether or not the presence of a monopectinate ctenidium can be taken to indicate a wholly or partially filter-feeding lifestyle is as yet unclear.

BIOLOGY

The majority of umboniine species inhabit soft substrata in relatively shallow water. None of the species discussed here have been found alive in water deeper

than 100 m and, except off oceanic islands, even their dead shells seem to be restricted to continental shelf depths (<200 m). Several species of *Ethminolia* appear to be inhabitants of shallow lagoonal environments, eg. *E. durbanensis* (Kilburn, 1977). Only *Lirularia* Dall, 1909 (placed in the related subfamily Lirulariinae by Hickman & McLean (1990), but here regarded as umboniine), is known to inhabit hard substrata (McLean 1986).

Biological observations on members of the Umboniinae are few. Fretter (1975) in her study of *Umbonium vestiarium* showed it to have a filter-feeding mode of life and to possess certain characteristic anatomical specialisations linked with this, many of which I have already mentioned. This was the first record of filter-feeding within the Archaeogastropoda. Since then it has been suggested that other genera may also filter-feed, including *Lirularia* (McLean 1986) and *Bankivia* (Hickman & McLean 1990).

Hickman (1985), in a comparative study, demonstrated that whilst filter-feeding may be characteristic of *Umbonium*, other umboniine genera such as *Ethminolia* are primarily deposit-feeders. Indeed, within the subfamily there seems, in terms of morphological adaptations toward filter-feeding, to be a graded series from the least specialised (? most primitive) and probably exclusively deposit-feeding genera such as *Ethalia*, to the most specialised (? more highly derived), almost entirely filter-feeding genera such as *Umbonium*. No southern African or Mozambican species evinces an entirely filter-feeding mode of life, although *Pseudominolia splendens* may combine this mode of feeding with deposit-feeding.

Most umboniine species appear to be efficient burrowers. This is undoubtedly linked with their preference for soft substrata and probably also plays an integral role in filter-feeding. The burrowing process relies primarily on the anchoring ability of the bifid propodium and has been described in *U. vestiarium* by both Fretter (1975) and Hickman (1985). In this species self-burial is rapid and clearly represents an adaptation to life on high energy sandy shores. Burrowing may be less significant in deeper water forms, but it seems probable that most are at least capable of partial burial; certainly all those examined have a bifid propodium. For several genera, however, behavioural observations are not available.

Kase (1989) hypothesised that the callus pad closing the umbilicus of *Umbonium* is an adaptation to an infaunal mode of life (cf. *Gaza* Watson, 1879 and many naticids), but gave no indication of the advantages that this might provide. It could be suggested that the lenticular form so produced would pass through the substratum more easily, but Kase has also shown that the umbilical region is totally covered by the foot when the animal is active. An alternative benefit may be that the callus adds weight to the base such that the shell will tend to come to rest base downward after 'swimming' (see below) or if dislodged by water movement (those species living in high energy, near-shore environments). It is also possible that thickening the shell around the umbilicus may help reduce predation by infaunal boring predators such as naticids. Despite this, however, species of *Natica* and *Polinices* have been shown to prey heavily upon populations of *U. vestiarium* in Malaysia (Berry 1984), boring through the base of the shell near the periphery (Savazzi & Reyment 1989).

A number of species exhibit what has been termed a twisting and leaping action

or a foot-thrashing action. In its mildest form this is used as a self-righting mechanism (Fretter 1975, Kikuchi & Doi 1987), but at its most vigorous it is an efficient escape response and the animal is capable of swimming rapidly away to a distance of as much as one meter. The behaviour is elicited by predatory starfish and flatworms (Kikuchi & Doi 1987), and predatory gastropods (Ansell 1969, Hickman 1985, Savazzi & Reyment 1989). This swimming escape response has been observed in all those local species that have been studied alive; it may also be artificially evoked by persistent irritation or disturbance. Kikuchi & Doi (1987) have shown the epipodial tentacles and posterior region of the foot to be the areas most sensitive to starfish. Similar behaviour occurs in many members of the Solariellinae (Herbert 1987), in the scissurellid genus *Sukashitrochus* (Haszprunar 1988) and in the neogastropod *Nassarius luteostomus* (Broderip & Sowerby, 1829) (Gonor 1965).

The sexes are separate and although the lips of the female urinogenital opening may be glandular (Fretter 1975), there are no secondary sex organs. Fertilisation is external and the developing larvae are almost certainly lecithotrophic, but development may be either benthic or planktonic. Berry (1986) has studied the reproduction of *U. vestiarium* and has shown that the eggs are broadcast into the sea and develop rapidly through the trochophore stage to become swimming veligers, which, after a pelagic phase of as little as 36–48 hrs, settle out and metamorphose. In contrast, Hadfield & Strathmann (1990) have shown *Lirularia succincta* (Carpenter, 1864) to have benthic (direct) development in which the larvae develop and metamorphose within a gelatinous egg mass attached to the underside of stones, without a planktonic phase.

ZOOGEOGRAPHY

Currently there is little published information concerning the zoogeography of the Umboniinae as a whole, or its constituent genera. The majority of genera and species occur in the Indo-West Pacific province in tropical and subtropical conditions, but a number are found in the temperate regions of Australia and New Zealand, and one species, *Monilea patricia* (Philippi, 1851) in the tropical eastern Pacific (Hickman & McLean 1990). The genus *Lirularia* occurs in cold-temperate to subtropical waters in both the north-eastern and north-western Pacific, but not in subarctic areas in-between. Additionally, there is evidence to suggest that certain eastern Atlantic taxa, such as *Solariella dereimsi* Dollfus, 1911, from off Senegal (see figure of living animal provided by Gofas *et al.* 1986) and *Solariella canaliculata* Smith, 1872, from off Benin (judging from a scanning electron-micrograph of the radula sent to me by Philippe Bouchet) are umboniine. Höisaeter (1968) has suggested that the northern European genus *Dikoleps* Höisaeter, 1968, belongs to the Umboniinae, but Hickman & McLean (1990) believe the similarities in radula morphology to be convergent and consider *Dikoleps* to be skeneiform (see also Ponder 1990 and Warén 1991).

Of the southern African and Mozambican species discussed herein, 2 (17%) are wide-ranging tropical/subtropical Indo-West Pacific species; 9 (75%) are western Indian Ocean species of which 5 (42% of the total) are possible south-east African endemics, having only been found off the Natal-Mozambique area. Only one

species (8%) is found in the Cape Province and then only in warm-temperate waters. This distribution pattern is in sharp contrast to that of the Solariellinae in which a large majority of locally occurring species are southern African endemics and more than 50% occur on the Agulhas Bank (Herbert 1987).

TAXONOMY

A thorough systematic revision of the subfamily Umboniinae including a computer-run cladistic analysis is beyond the scope of an essentially regional study such as this. A more global investigation including genera not represented in southern Africa is being undertaken by Hickman (personal communication). Nevertheless, a number of observations made during the course of the present revision are of considerable phylogenetic significance with regard to the subfamily as a whole and merit further consideration. Hickman & McLean (1990) united their subfamilies Halistylinae, Lirulariinae and Umboniinae in an informal group, basing this on similarities in ctenidial form and radula morphology (specifically a monopectinate ctenidium and a radula with a reduced central field). However, it would appear that much of this similarity is superficial or homoplasious in respect of the Halistylinae. Although the ctenidium is apparently monopectinate and the teeth of central field of the radula reduced, the ctenidial leaflets are not elongate and lack swollen tips, the marginal teeth of the radula are very long and slender with short cusps, the foot is not anteriorly bifid, the left neck lobe is undivided, there are five pairs of epipodial tentacles and subterminal snout papillae are lacking. In contrast, the Lirulariinae and Umboniinae share several derived character states and are almost certainly closely related. One of the premises upon which Hickman & McLean based their definition of this group of trochids was that all members possess a monopectinate ctenidium. The anatomical observations reported herein show that this is not true in every case. I have examined a number of species of *Ethalia*, *Ethminolia* and *Monilea* (all belonging to Hickman & McLean's tribe Monileini) and found all to possess a bipectinate ctenidium with a long afferent membrane typical of more advanced trochid subfamilies. This has important consequences in terms of the interpretation of the phylogeny of the group and the classification to be drawn from this.

The Monileini as constituted by Hickman & McLean contains taxa showing a variety of character states and clearly needs to be looked at in greater detail. Taxa such as *Zethalia* Finlay, 1926 and *Antisolarium* Finlay, 1926, have a monopectinate ctenidium and a number of other derived anatomical features not present in *Monilea* (Walsby & Morton 1982 and personal observation), and should not be referred to this tribe. I propose a more restricted use of the taxon Monileini to encompass umboniines retaining a relatively unspecialised external anatomy (wide forehead, prominent snout and simple digitate left neck lobe) and a bipectinate ctenidium. It might be argued that such species should be removed from the Umboniinae, but they share several apomorphies of the radula and external anatomy which undoubtedly ally them with this subfamily. It is clear that they represent a level of anatomical complexity linking the more highly derived members of the subfamily with less specialised forms such as the Trochinae.

The presence of a bipectinate ctenidium in the Monileini necessitates a reassessment of the systematic status of the Lirulariinae. To maintain this group as a distinct subfamily (cf. Hickman & McLean 1990) in the light of the above, is to suggest that a monopectinate ctenidium of similar structure has evolved independently on two occasions within what amount to closely related taxa. This is most unlikely. More probable is that lirulariine and umboniine taxa share a more recent common ancestor with each other than either do with monileine forms. If this is indeed the case, then the Lirulariinae must be down-graded and classified within the subfamily Umboniinae. The differences reported by Hickman & Mclean (1990) between *Lirularia* and umboniine taxa are all minor when compared with the development of a monopectinate ctenidium.

Subdivision of the Umboniinae into tribes is problematic and has the potential for the creation of a profusion of monogeneric taxa. In the present study I have utilised only two tribes, the Monileini and Umboniini, for southern African material. Genera with a bipectinate ctenidium are referred to the Monileini and those with a monopectinate ctenidium to the Umboniini. This is a simplistic approach, but a pragmatic one in view of the present incompleteness of our knowledge regarding the group.

Application of genera and subgenera within the Umboniinae has been far from settled for a long time. Many of the supraspecific taxa that have been described were given woefully inadequate diagnoses and have never been studied in detail. I have experienced considerable difficulty in assigning southern African species to appropriate genera. As will be discussed later, there is much intergrading of shell characters between genera as well as possible convergences, and yet to date it is largely these characters upon which the genera have been based (see remarks regarding *Ethminolia*). This situation can only be remedied by examination of other characters such as those of the radula, external anatomy, ctenidium and possibly operculum. It is important that such studies be conducted, whenever possible, on the type species of the genera concerned.

One of the most widespread misconceptions concerning the subfamily has centred on the genus *Minolia* A. Adams, 1860, which has been used extensively as a 'hold-all' taxon for a wide range of Indo-West Pacific umboniine species. For many years *Minolia* was thought to possess a radula with reduced teeth in the central field, largely on the basis of Thiele's observations on the radulae of *'Minolia' vitiliginea* (Menke, 1843) and *'Minolia' casta* (G. & H. Nevill, 1874) (Thiele 1891 1924). The type species of *Minolia*, *M. punctata* A. Adams, 1860, however, has since been shown to have a solarielline radula (Tsuchida & Kitao 1986). *Minolia* cannot therefore be used for any umboniine species. A number of other taxa, eg. *Priotrochus* Fischer, 1879, and *Callumbonella* Thiele, 1924, have been included in the subfamily by prior authors, but in fact belong elsewhere (Herbert 1988 and unpublished observation).

Of the species discussed herein, *Solariella splendens* Sowerby, 1897, *S. sculpta* Sowerby, 1897, and *Margarita articulata* Gould, 1861, have frequently been referred to *Minolia*, but all have a radula with cuspless median teeth. The same is also almost certainly true of *Solariella durbanensis* Kilburn, 1977, and all are here referred to the Umboniinae. The only other umboniine genus legitimately

recorded to date from southern Africa is *Ethalia* H. & A. Adams, 1854, but until now this was not known south of Mozambique (Kilburn 1977). Previous records of *Ethalia* from South Africa (eg. *E. africana* Smith, 1904) refer to species of *Teinostoma* H. & A. Adams, 1854 (Vitrinellidae). *Monilea spuria* Gould, 1861, described from False Bay, is a *Cinysca* Kilburn, 1970 (Turbinidae: Liotiinae) [in fact, *Cinysca granulosa* (Krauss, 1848) *fide* Barnard 1963].

The northern Indian Ocean species *Umbonium vestiarium* was recorded from Durban by Sowerby (1897), from the 'Cape of Good Hope' by Bartsch (1915) and from southern Transkei by Barnard (1963). Kilburn (1977) has discussed these records and concluded that the species does not in fact occur in southern Africa. Krauss (1848) recorded material sent to him, supposedly from the Cape coast, by Baron von Ludwig as *Bankivia varians* Beck [= *B. fasciata* (Menke, 1830) from southern Australia]. The reliability of this record was questioned as early as 1874 by Von Martens who noted that Von Ludwig had also received natural history specimens from Australia. Von Martens rightly stated that the species should not be considered part of the South African fauna.

Family: Trochidae Rafinesque-Schmaltz, 1815

Subfamily: Umboniinae H. & A. Adams, 1854

Umboniinae H. & A. Adams, 1854: 407 [nominotypical genus *Umbonium* Link, 1807].

Diagnosis: Teeth of central field of radula reduced, marginals well developed and numerous, latero-marginal plate present; protoconch small (<250 μm in diameter) and beaked; teleoconch frequently with scratch-like axial microsculpture; snout with subterminal papillae; forehead frequently narrow or absent and snout reduced in size (not Monileini); eye stalks more or less elongate, curving up under shell margin during life, eyes large, terminal (except *Bankivia* and *Leiopyrga*); left neck lobe variously modified to form a particle exclusion filter, greatly hypertrophied in certain genera (eg. *Umbonium*); foot anteriorly bifid; ctenidium long, extending whole length of mantle cavity; ctenidial filaments elongate, with swollen tips and prominent bursicles, filaments on left side of ctenidial axis reduced or absent; afferent ctenidial membrane long, ctenidium sometimes attached to mantle skirt throughout its length.

Provision of a diagnosis for the Umboniinae is problematic. Many features such as the elaboration of the left neck lobe, elongation of the eye stalks, reduction of the snout and monopectinate structure of the ctenidium, whilst they are derived characters typical of some genera within the subfamily, are not characteristic of all. Nevertheless all genera here discussed show a combination of umboniine apomorphies such that they are clearly referable to this subfamily.

Key to genera of Umboniinae in southern Africa and Mozambique

1 Umbilicus with a funicle and/or heavy callus deposit; ctenidium bipectinate ... **Ethalia**

– Umbilicus without funicle or callus deposit; ctenidium bipectinate or monopectinate 2

2 Shell relatively high, turbiniform (L/D 0,7–1,1); digitations of left neck lobe branched; snout projecting beneath cephalic tentacles, no obvious forehead between cephalic tentacles; ctenidium monopectinate; operculum rendered lustreless by close-set, microscopic spiral lirae ..... **Pseudominolia**

– Shell depressed, trochoid-turbiniform to turbiniform (L/D <0,83); left neck lobe with unbranched digitations; cephalic tentacles separated by distinct forehead; ctenidium bipectinate or monopectinate; operculum glossy, lacking microscopic spiral lirae 3

3 Shell trochoid-turbiniform, periphery well below mid-whorl; sculptured primarily by close-set spiral lire (not keel-like cords), subsutural lira strong and frequently beaded on later whorls; basal sculpture weak except around umbilicus; ctenidium monopectinate ..... **Inkaba**

– Shell not as above; ctenidium bipectinate ..... **Ethminolia**

Tribe Monileini Hickman & McLean, 1990

Diagnosis: Umboniinae in which the ctenidium is bipectinate and which have a relatively broad snout and a distinct forehead between the cephalic tentacles. Radula ribbon long, teeth of central field retaining relatively well defined basal plates and sometimes traces of tooth shafts. Shell usually depressed, umbilicus frequently, but not invariably with a funicle and/or heavy callus deposit.

Genus *Ethalia* H. & A. Adams, 1854

Ethalia H. & A. Adams, 1854: 409; Schepman, 1908: 74, fig. 3 (radula); Hickman, 1980: pl. 1, fig. a; 1984: fig. 18a (radula), type species (s. d. Pilsbry, 1889) *Rotella guamensis* Quoy & Gaimard, 1834.

Liotrochus Fischer, 1878: 207, type species (monotypy) *Rotella montrouzieri* Souverbie, 1860 (= *Rotella guamensis* Quoy & Gaimard, 1834, *fide* Pilsbry, 1889).

Diagnosis: Shell resembling that of *Umbonium* Link, 1807, but with basal callus deposit usually only partly filling umbilicus; radula ribbon long, base plates of rachidian and laterals remaining relatively well developed; external anatomy unspecialised with distinct forehead between cephalic tentacles, unbranched left neck lobe digits and relatively short eye stalks; ctenidium bipectinate for most of its length, terminal portion free; operculum lacking microscopic spiral lirae.

Radula: Formula ∞ + (1) + 5 + 1 + 5 + (1) + ∞, 70–80 transverse rows. Schepman (1908: text fig. 3), Hickman (1980: pl. 1a, 1984: fig. 18a) and Hickman & McLean (1990: fig. 85c, f) have figured the radula of the type species and that of local species is similar. Although typically umboniine in the absence of cusps on the rachidian and laterals, it is less reduced than in most other umboniine genera. The basal plates of the teeth remain relatively thick and the structure as a whole is much longer. The first marginal is broad, has a reduced cusp and doubtlessly functions as a latero-marginal plate. The remaining inner marginals each possess a single large spatulate cusp with a prominent thumb-like denticle proximally on its outer edge (occasionally there may be two such denticles). The number of denticles increases on the outer marginals.

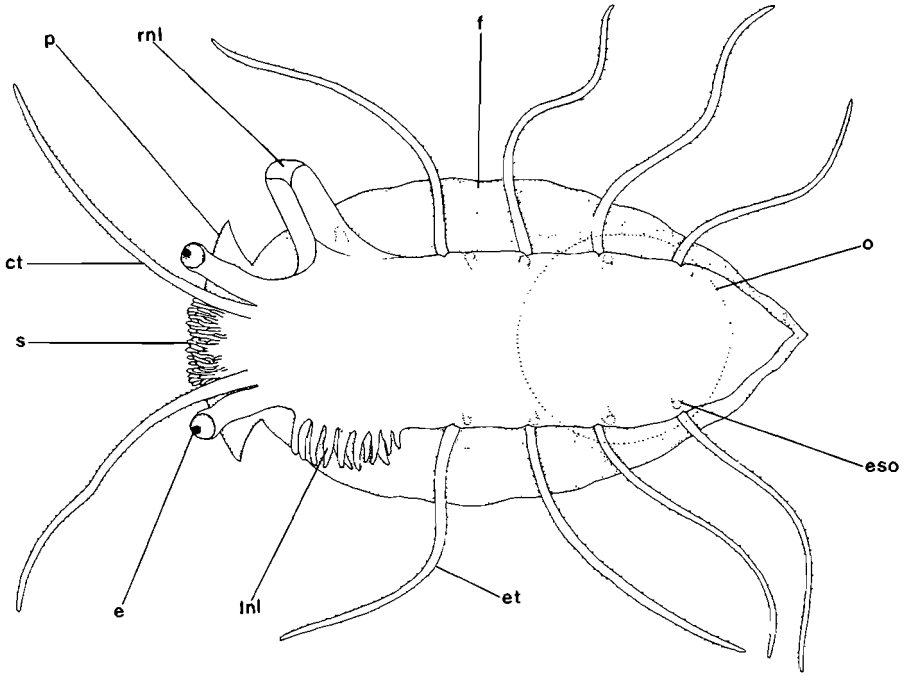
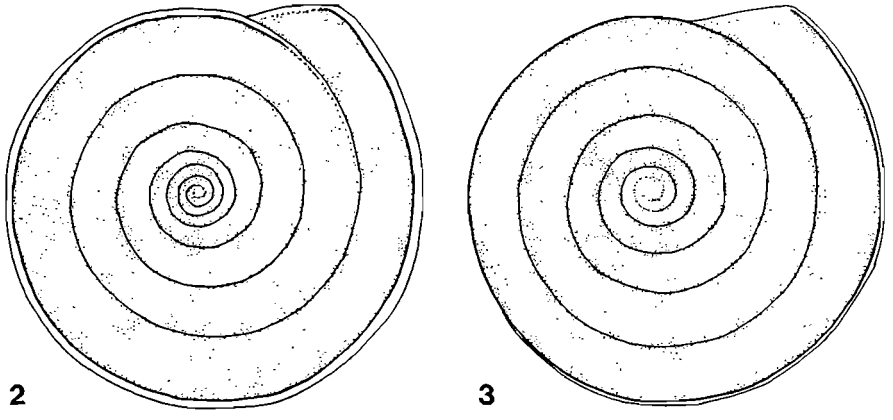


Fig. 1. *Ethalia gilchristae* sp. n. Diagrammatic representation of external anatomy: ct, cephalic tentacle; e, eye; eso, epipodial sense organ; et, epipodial tentacle; f, foot; lnl, left neck lobe; o, operculum; p, propodium; rnl, right neck lobe; s, snout.

External anatomy (Fig. 1): The external anatomy of *E. guamensis* has been figured by Hickman & McLean (1990). That of *E. gilchristae*, described in detail below, is similar except that distinct cephalic lappets are lacking. Evidently *Ethalia* retains a relatively unspecialised external anatomy. Although it possesses several of the derived characters typical of the subfamily as a whole (eg. a subterminally papillate snout, a bifid propodium and a long ctenidium with elongate filaments), it retains primitive characters such as simple left neck lobe digits, relatively short eye stalks, a distinct forehead and well developed snout (Fig. 33), and filaments on both sides of the ctenidial axis (Fig. 34).

Operculum (Figs 2–3): Corneous, multispiral, concave, comparatively thick, but with relatively few whorls and a relatively wide growing margin; nucleus central; no microscopic spiral lirae on exterior surface; overlap between whorls narrow, peripheral fringe not obviously radially striate.

Remarks: *Ethalia* with its depressed, glossy shell and calloused umbilicus, superficially resembles *Umbonium* and was in fact regarded as a subgenus of the latter by some earlier authors (Keen, 1960). However, the anatomical differences existing between the two are considerable and are doubtlessly of greater phylogenetic significance. The similarities in shell form may have resulted, at least partly, from convergence and may simply reflect adaptation to a semi-infaunal, burrowing mode of life (cf. naticids).



Figs 2–3. Operculum of *Ethalia*: 2, *E. gilchristae* sp. n., diameter 4,8 mm; 3, *E. carneolata* Melvill, 1897, diameter 5,3 mm.

Species within this genus show a whole range of funicular development and callus deposition (Fig. 4). In the least well developed (? least derived) state the funicle is narrow and there is little callus deposition (*E. electra* sp. n., Fig. 4f) – a state somewhat similar to species supposedly referable to *Talopena* Iredale, 1918, eg. *Talopena gloriola* Iredale, 1929 (Fig. 131). Intermediate states include species with a relatively weak funicle, but distinct, tongue-like callus deposit (*E. carneolata* (Figs 4a–b) and *'Minolia' edithae* Melvill, 1891). The most well developed state is present in species such as *E. guamensis* and *E. bysma* sp. n. (Fig. 4e), which have a thick funicle and heavy callus deposition such that the umbilicus is almost closed off. It is these umbilical features combined with the form and strength of the spiral sculpture that are the most useful characters in species discrimination.

Key to species of *Ethalia* in southern Africa and Mozambique

1 Shell smooth and glossy, spiral sculpture of relatively few widely spaced striae; umbilicus open, but with tongue-like callus deposit where columella meets paries ..... **carneolata**
– Shell not as above 2

2 Umbilicus almost closed by thick callus plug at end of well developed funicle; adapical surface sculptured by fine incised spiral striae rather than raised lirae, base with numerous close-set spiral striae ..... **bysma**
– Umbilical funicle less well developed, umbilicus remaining open; adapical surface sculptured by raised spiral lirae rather than incised striae, base with fewer, more widely spaced striae 3

3 Umbilical funicle well defined, but narrow and with little callus deposition; whorls with shoulder angulation; spiral sculpture relatively coarse, intervals between lirae wider than lirae themselves ..... **electra**

– Umbilical funicle broad and with distinct callus deposit spreading to parietal region; whorls lacking shoulder angulation; spiral sculpture close-set, lirae wider than their intervals ..... **gilchristae**

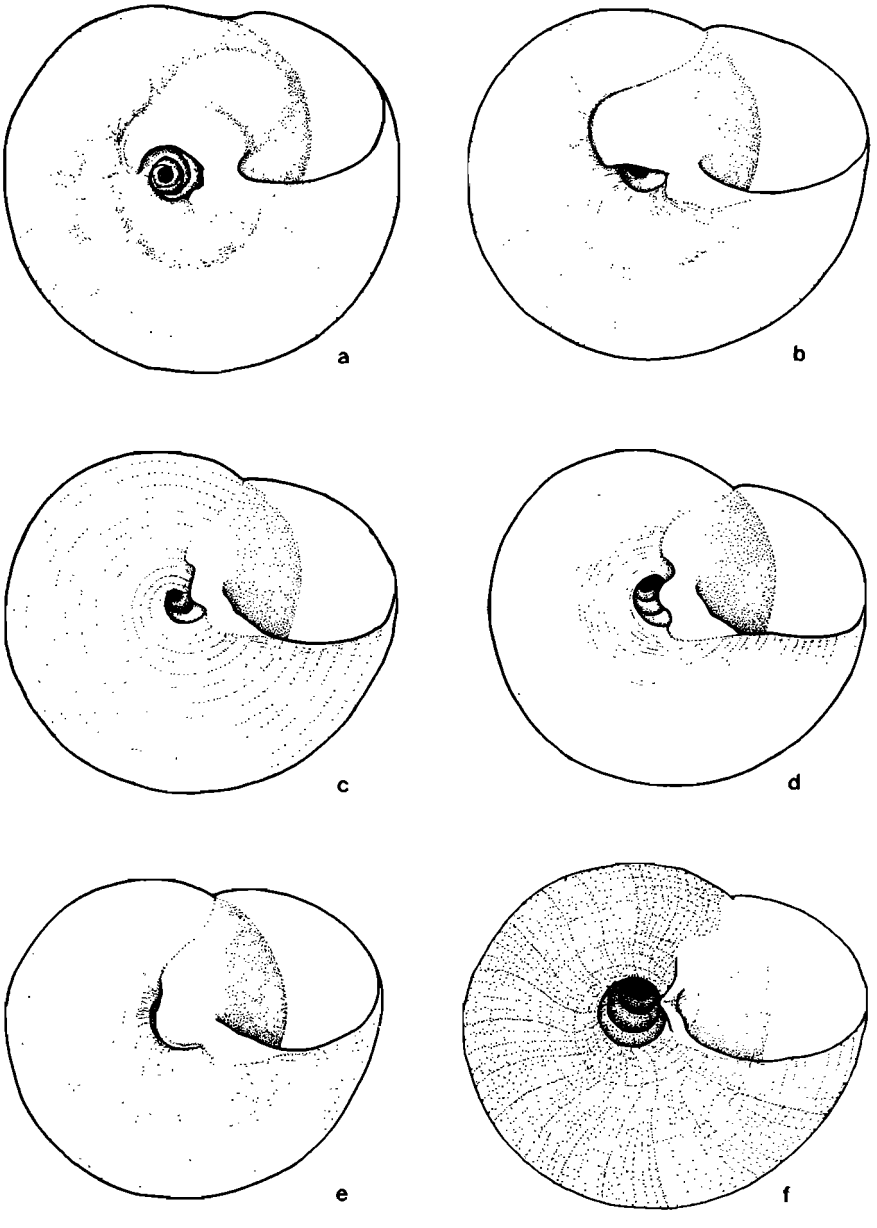


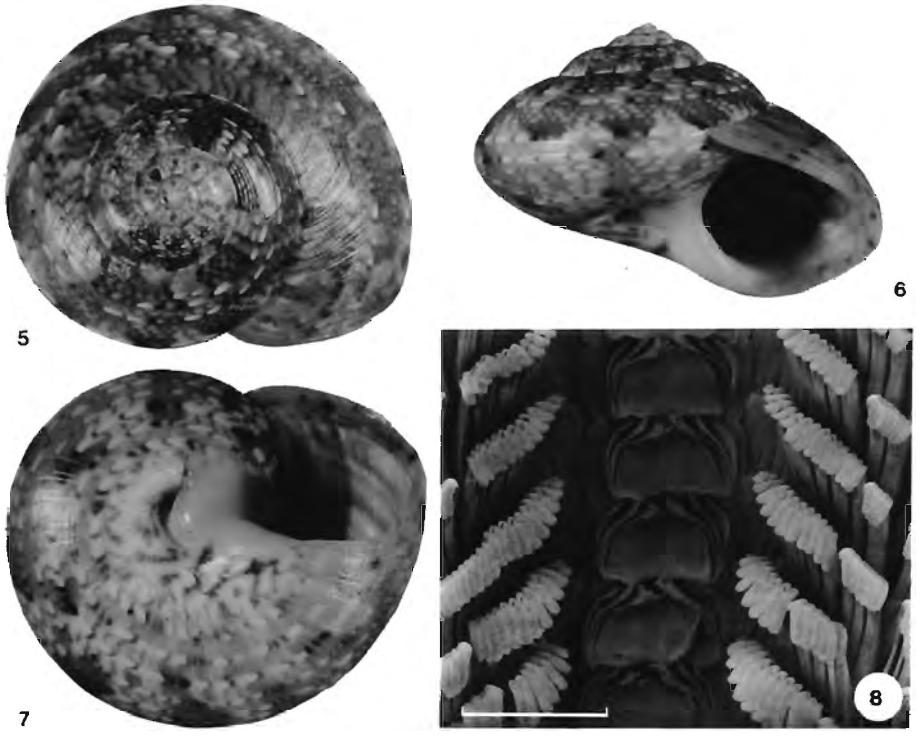
Fig. 4. Basal views of *Ethalia* species. a, *E. carneolata* Melvill, 1897 (NMSA D7971); b, *E. carneolata*, Mozambique specimen (NMSA J9626); c, *E. gilchristae* sp. n. holotype; d, *E. minolina* Melvill, 1897, holotype; e, *E. bysma* sp. n. holotype; f, *E. electra* sp. n. holotype.

Ethalia bysma sp. n.

Figs 4e, 5–8; Map 1.

Diagnosis: Shell similar to that of *E. gilchristae* sp. n., but spiral sculpture on apical surface finer and base with numerous close-set spiral striae; umbilicus almost completely closed by funiclular callus.

Description: Shell depressed turbiniform (L/D = 0,68–0,75); relatively solid, lustreless; teleoconch of up to 5,5 whorls; periphery roundly angular, at or just below mid-whorl; suture level. First whorl evidently smooth, remainder of apical surface sculptured by numerous, fine, close-set, spiral striae, becoming more numerous and close-set with growth; base with similar sculpture. Axial sculpture of numerous fine collabral growth-lines, some relatively strong, particularly on apical surface of body whorl. Shell umbilicate, but umbilicus almost completely closed off by callus at end of well developed funicle, leaving only an umbilical chink; umbilical margin thickened but not well differentiated from base; axial sculpture coarser at edge of umbilicus. Aperture subquadrate; columella with heavy, somewhat glossy callus deposit at end of umbilical funicle, also at end of thickened umbilical margin and at junction with parietal region; callus present as three lobes, but funicular and parietal regions tending to merge into one, some intraspecific variation in this respect; parietal callus spreading as a thin

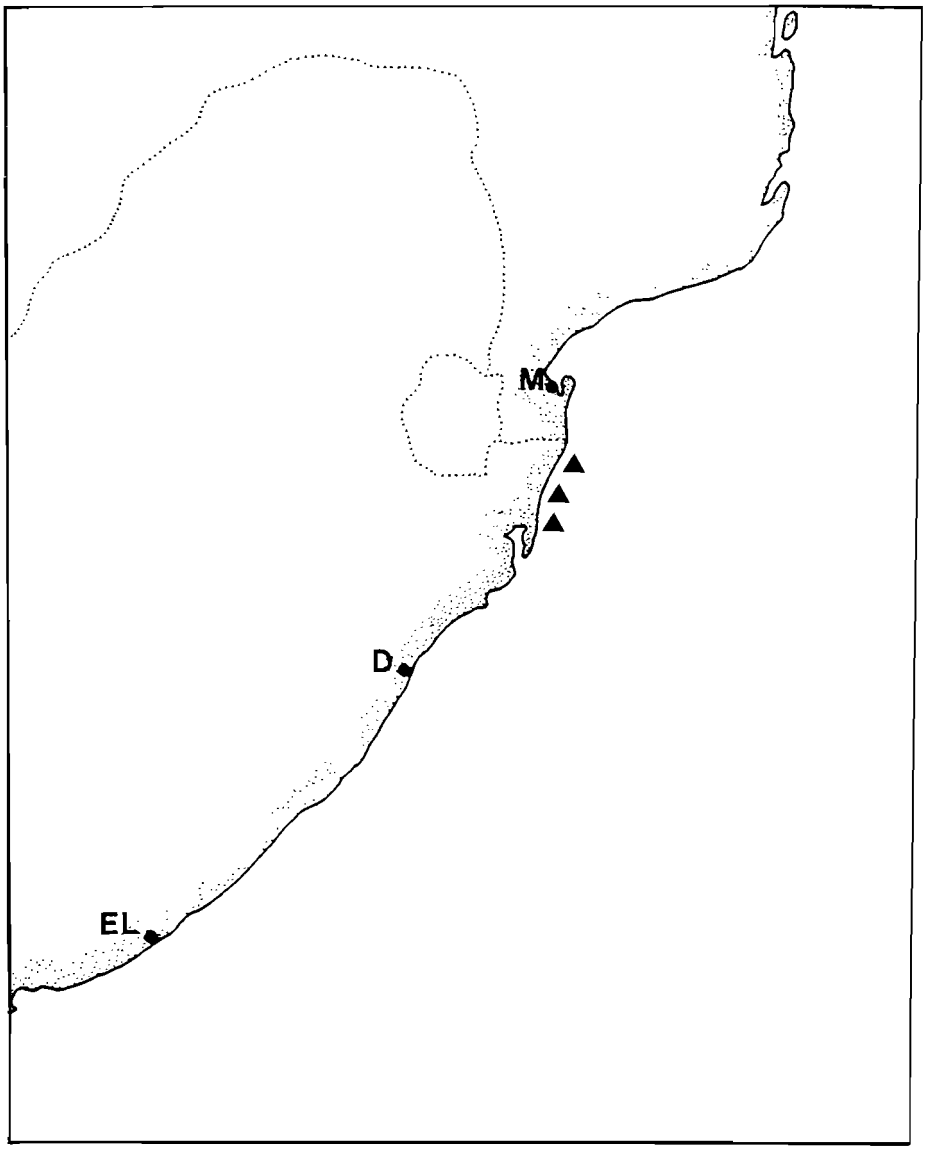


Figs 5–8. *Ethalia bysma* sp. n. 5–7, holotype, diameter 11,7 mm (NMSA E1685/T67); 8, radula, *ex* paratype 1, bar = 100 μm.

translucent layer over paries toward outer lip, but not extending far onto base beyond aperture; outer lip smooth, strongly prosocline above periphery, orthocline or nearly so beneath; interior nacreous.

Protoconch: Not examined under SEM, but evidently similar to that of other *Ethalia* species; diameter 200–240 μm.

Colour: Variable; ground colour greyish-white mottled or washed (sometimes heavily) with shades of pink to red with green-brown bands or blotches and



Map 1. South-eastern Africa showing distribution of *Ethalia bysma* sp. n.; each black triangle represents one or more records.

numerous whitish flecks; white flecks alternate with darker colours to form articulated spiral lines; umbilicus white, margin with dark red to reddish-brown markings of variable shape.

Dimensions: Holotype, diameter 11,7 mm, length 7,9 mm; paratype 2 (largest specimen), diameter 11,9 mm, length 8,9;an16 mm.

Operculum: As in *E. gilchristae* sp. n.

Radula (Fig. 8): Like that of *E. gilchristae* sp. n.

External anatomy: Like that of *E. gilchristae* sp. n.

Distribution: Zululand; Boteler Point to Gipsy Hill (27°00′ to 27°50′S), 50–110 m (living specimens 50–70 m).

Type material (all dredged NMDP): Holotype, NMSA E1685/T67, off Boteler Point, northern Zululand (27°0,5′S:32°54,7′E), living, 50 m, coral rubble and dead *Lithothamnion*; paratype 1, NMSA E1698/T52, off Boteler Point, northern Zululand, living, 70 m, coral rubble; paratype 2, NMSA D6808/T53, off Boteler Point, northern Zululand, living, 50 m, coral rubble, sponges; paratype 3, NMSA E3714/T247, N.E. of Gipsy Hill, Zululand, dead, 110 m, sponge, stones; paratype 4, NMSA S3373/T367, S.E. of Lala Neck, northern Zululand, dead, 92–97 m, muddy sand; paratype 5, NMSA S4184/T730, off Boteler Point, Zululand, dead, 58–61 m, sand, pebbles.

Remarks: This species most closely resembles *E. minolina* Melvill, 1897, from the Persian Gulf (holotype BMNH 1879.7.30.108, Figs 125–127), particularly in the form of its spiral sculpture. The present species is distinguished by the well developed funicle which almost completely blocks the umbilicus. *E. guamensis selenomphala* Pilsbry, 1905, from Japan, has a similarly large umbilical plug, but the shell is glossy and more finely sculptured, and has a tongue-like parietal callus extending onto the base well beyond the limits of the aperture.

Etymology: *Bysma* Gr., (f) a plug or bung, referring to the blocked umbilicus.

Ethalia carneolata Melvill, 1897

Figs 3, 4a b, 9–22; Map 2

Ethalia carneolata Melvill, 1897: 19, pl. 7, figs 24 & 26 (not 25 & 26 as given); Standen & Leicester, 1906: 270; Smythe, 1982: 37; Glayzer *et al.*, 1984: 318; Kaicher, 1990: 5698. Type loc.: Bass Island (see notes on type material), 10 fathoms (= 18,3 m), (also Shaikh Shuahib Island = Jazireh-ye Sheykh Sho'eyb, Persian Gulf).

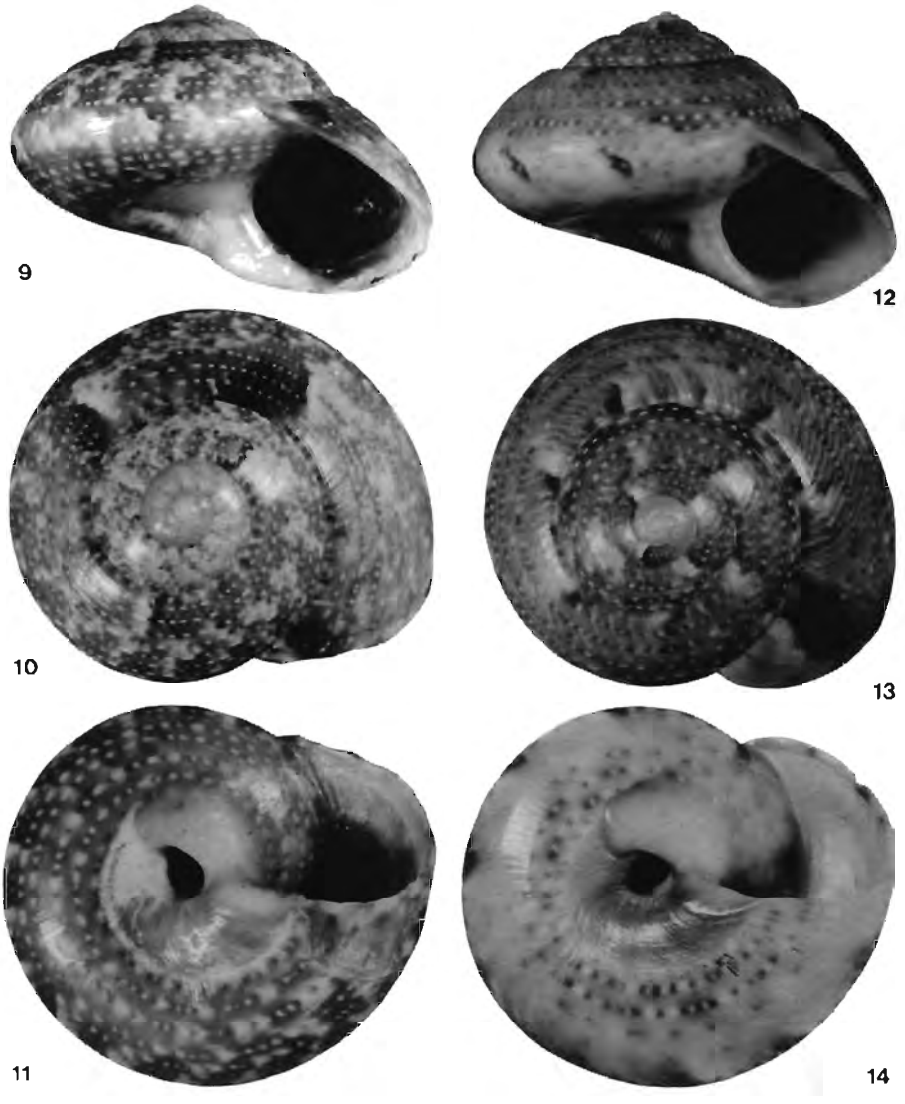
Rotella carneolata; Shopland, 1902: 176.

Ethalia carneolata var. *rubrostrigata* Melvill, 1904: 80, pl. 8, fig. 3; Kaicher, 1990: 5697. Type loc.: Dabai [= Dubai], Persian Gulf.

Ethalia striolata (*non* A. Adams, 1855); Kilburn, 1977: 176.

Diagnosis: Shell glossy, spiral sculpture comprising at most fine, widely spaced striae on apical surface; umbilicus open, lacking a distinct funicle, but with strongly thickened margin; callus deposit bilobed, parietal element relatively large, linguiform, and partly obscuring umbilicus.

Description: Shell depressed, trochoid-turbiniform to turbiniform (L/D = 0,65–0,78), smooth and glossy, relatively solid; teleoconch of up to 6 whorls; whorls somewhat flattened; periphery roundly angular, just below mid-whorl;



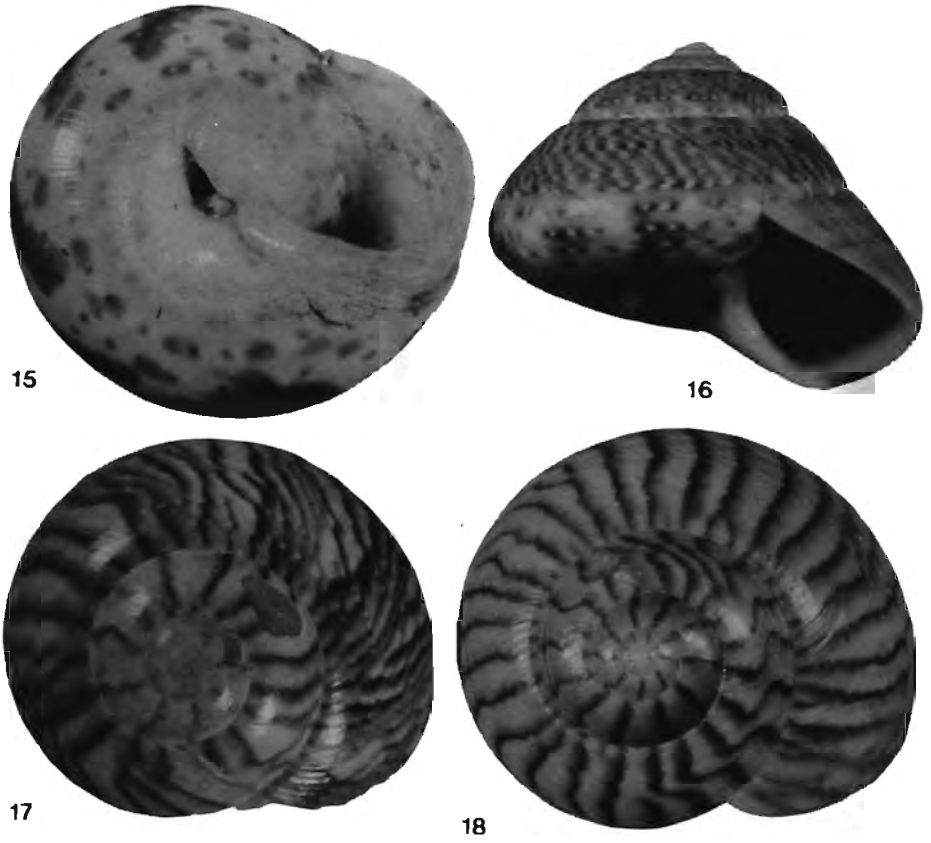
Figs 9–14. *Ethalia carneolata* Melvill, 1897. 9–11, syntype from Bass Island, diameter 10,2 mm (BMNH 1897.7.30.107); 12–14, specimen from off Kosi Bay, northern Zululand, diameter 14,4 mm (NMSA D7971).

suture slightly sunken. Early whorls evidently smooth, fine incised striae developing during second whorl and becoming more numerous with growth; number of striae on body whorl variable, sometimes over 20, but usually less than 10, often less obvious toward suture; base without spiral striae; axial sculpture comprising only microscopic, collabral growth-lines. Umbilicus open, but partially obscured by callus deposit at junction of parietal and columella regions; callus linguiform (Figs 11, 14), extending over parietal region well beyond apertural margin, white, microscopically granular and lustreless.

Umbilical margin markedly thickened by callus ridge; ridge sculptured by numerous very fine, curved growth-lines and at most fine, irregularly spaced spiral striae; growth-lines distinctly kinked where marginal thickening meets base. Umbilicus funiculate, linguiform callus forming at end of funicle; callus deposits of columella region jointly forming a bilobed structure (Fig. 14). Umbilicus generally wider and parietal callus smaller in Zululand specimens; some specimens from Mozambique with callus almost filling umbilicus (Fig. 15). Aperture subquadrate; columella lip edged with nacre; outer lip smooth, strongly prosocline above periphery, orthocline or nearly so on base; interior nacreous.

Protoconch (Fig. 19): Diameter 200–240 μm, apex weakly beaked, connection with terminal lip well developed, surface with faint signs of sculpture.

Colour: Very variably patterned; overall colour whitish to fawn, brown, pink or red, but composed of spots blotches and lines of numerous shades within these colours; sometimes a combination of several colours, often with narrow spiral



Figs 15–18. *Ethalia carneolata* Melvill, 1897. 15, shallow-water Mozambique specimen with narrow umbilicus and increased callus deposition, diameter 12,1 mm (NMSA J9624); 16, elevated specimen, diameter 16,5 mm (NMSA D7140); 17, syntype of *Ethalia carneolata* var. *rubrostrigata* Melvill, 1904, diameter 8,9;an16 mm (BMNH 1905.6.6.4); 18, *rubrostrigata* colour form from northern Zululand, diameter 11,6 mm (NMSA D9222).

lines of white and brownish dots or dashes; base usually more coarsely patterned than apical surface; umbilical margin frequently a pale shade of brown. Some specimens more or less uniform in colour, others with a distinct pattern of radiating rays of colour (cf. var. *rubrostrigata* Melvill, 1904, Figs 17–18).

Dimensions: Largest NMSA specimen, diameter 16,5 mm, length 12,9 mm.

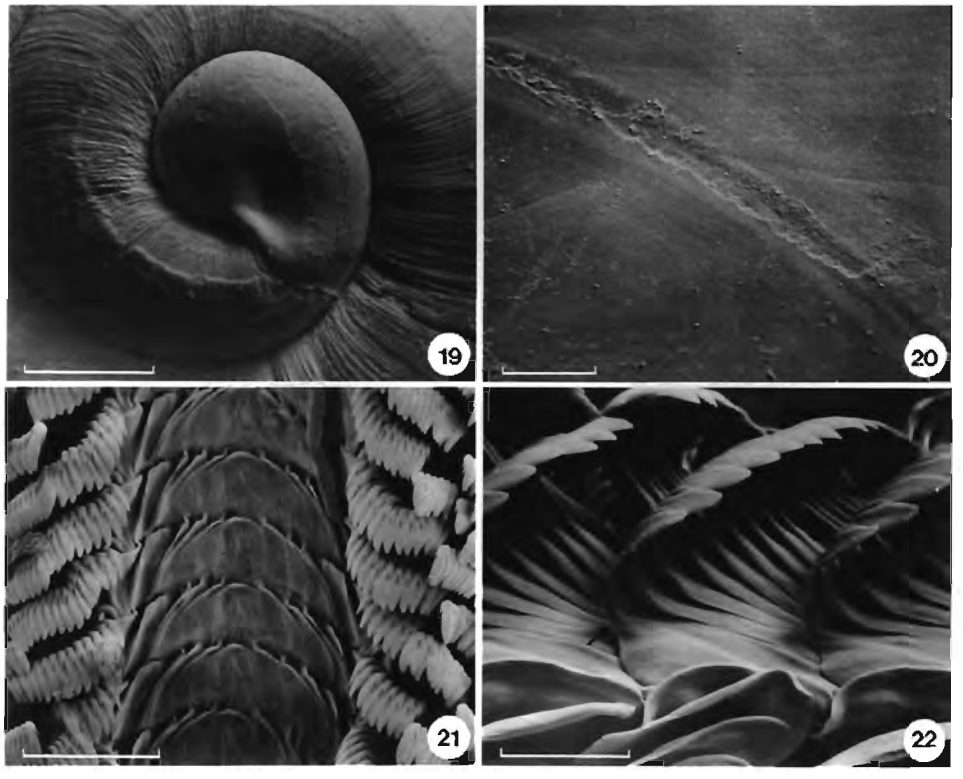
Operculum (Fig. 3): Like that of *E. gilchristae*.

Radula (Figs 21–22): Long, 70–80 transverse rows; similar in form to that of *E. gilchristae*, but with basal plates of rachidian and inner laterals thinner and less well defined; marginals sometimes with two denticles on outer edge.

External anatomy: Like that of *E. gilchristae*, but animal paler and lacking white pigment spots.

Distribution: Western Indian Ocean; Persian Gulf to Zululand, Comores, Madagascar, Réunion Island and Gulf of Manaar. Beach-drift to 60 m (living specimens 6–58 m, fine sandy substrata). A single dead juvenile dredged at 300–450 m off the Comores presumably originated in shallower water.

Regional locality data (all NMSA, dredged NMDP, dead, unless indicated



Figs 19–22. *Ethalia carneolata* Melvill, 1897. 19, protoconch, bar = 100 μm (NMSA E1368); 20, operculum, bar = 100 μm (NMSA D7236); 21, radula, central field and inner marginals, bar = 100 μm (NMSA D7236); 22, latero-marginal area of radula showing broad base and reduced cusp of first marginal (arrow), bar = 40 μm (NMSA D7236).

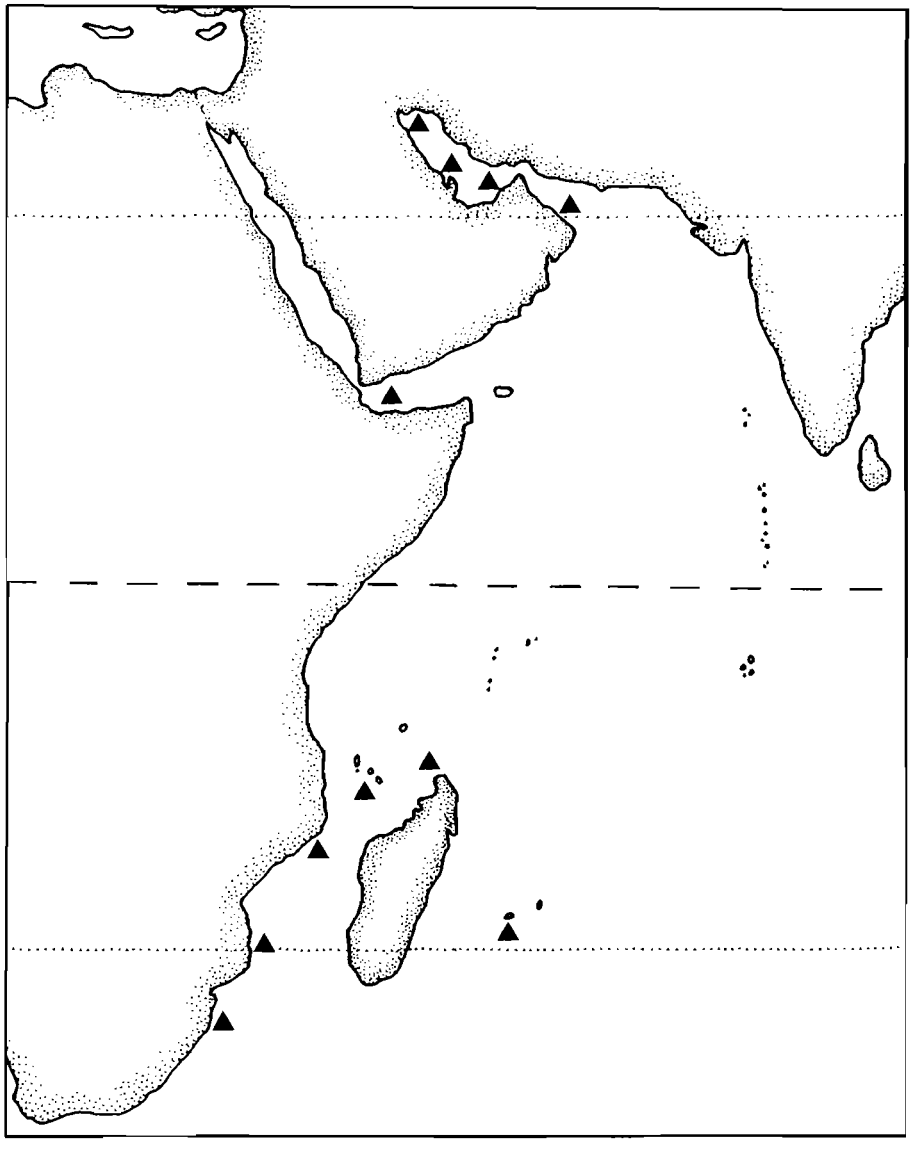
otherwise): NORTHERN MOZAMBIQUE: S.W. Lunga Bay, dredged *ca* 8 m, K. Grosch (H291); S.W. Nacala Bay, S. of Old Nacala, K. Grosch (H4023); S.W. Conducia Bay, N.W. of Choca, K. Grosch (H290). SOUTHERN MOZAMBIQUE: Bazaruto Archipelago: ½ mile west of Santa Carolina Is., living, dredged *ca* 6 m, sand and shell debris, E. Roscoe (G7114, J9625, J9629); W. of Santa Carolina Is., living, dredged *ca* 10 m, E. Roscoe (J9628); Bazaruto Archipelago, various localities, E. Roscoe (G4625, J9626, J9627, F9942). ZULULAND: N.E. of Kosi Bay, living, 52–53 m, coarse sand (S4957); off Kosi River mouth, living, 45 m, fine muddy sand (D6028); do, 30 m, coarse sand (D7639); do, 42 m, fine sand (S3797); do, 50 m, medium sand, algae (D6181); S.E. of Kosi River mouth, living, 50 m, fine slightly muddy sand (D9222); do, living, 50 m, fine sand, shell rubble, *Codium* (D7236); do, living, 50 m, fine muddy sand (D7849); do, living, 50 m, fine sand, shells (D8366, D8408); do, living, 50 m, coarse sand, shells (D6983); do, 45–50 m, fine sand, algae, gorgonians (E1368, D8907); do, living, 40 m, fine sand (D8266, D8805, E2925); do, living, 40 m, shell rubble (D8139, D7971); off Hully Point, living, 35 m, few shells, algae (D9075); do, living, 30–40 m, fine muddy sand (E812); off Gobey's Point, 55–60 m, sand, shell rubble (D7183); off Jesser Point, 50 m, fine sand (D7334); do, living, 40 m, shell rubble (D7140); do, 42 m, medium sand (E811); do, living, 52–58 m, medium sand, (D8526); off Sodwana Bay, 50 m, shell grit, dredged CSIR Water Research (S3146); off Gipsy Hill, 48 m, fine sand (E3448).

Extralimital locality data: PERSIAN GULF: 12 nautical miles E.N.E. of Bahrain Lightship, living, 23,5 m, shell gravel, dredged G. Thorson (ZMUC); Stiffer's Bank (26°27'N:53°8'E), 33 m, shells and coral gravel, dredged G. Thorson (ZMUC). OMAN: Muscat, H. Burnup coll'n (NMSA G4319); do, *ex* M. V. Lebour, H. Becker coll'n (NMSA J1112). COMORES: Mayotte, W. Passe Boueni, 300–450 m, dredged BENTHEDI 1977, st. 49 (MNHN). MADAGASCAR: Ifaty Lagoon, 6 m, J. Drivas (NMSA K2757). RÉUNION ISLAND: off Possession, living, 54 m, sand, J. Drivas (NMSA K2758).

Type material: The BMNH has two syntype lots. The first (BMNH 1897.7.30.107) contains a single specimen from Bass Island (Figs 9–11) and the second (BMNH 1899.2.18.12–13) contains two specimens from the Persian Gulf. The latter, however, cannot be regarded as type material as they were discussed not as part of the original description, but only in an added note. The type status of the Bass Is. specimen is also uncertain as it far exceeds the measurements given by Melvill (diameter 10,2 mm, length 7,0 mm compared with Melvill's 7,0 mm and 4,0 mm respectively). I have been unable to establish the location of Bass Island within the Arabian Sea, Persian Gulf, Gulf of Oman area. Townsend did not mention it in his notes (Townsend 1928). Two syntypes of the variety *rubrostrigata* Melvill, 1904, are present in the NMWC (1955.158.144) and one in the BMNH (1905.6.6.4), the latter is the figured specimen and it is here refigured and designated varietal lectotype (Fig. 17).

Remarks: This species is somewhat variable with regard to the development of the parietal lobe of the basal callus deposit. Whilst this is to some extent dependent on the age of the individual, specimens from Zululand, most of which were collected in

deeper water (± 50 m), generally have a smaller callus which obscures less of the umbilicus. This difference is further exaggerated by the fact that Zululand specimens also tend to have a wider umbilicus (compare Figs 11 and 14). The density of spiral striae on the adapical surface is likewise variable. Melvill's Bass Is. specimen and several NMSA specimens from Oman and Réunion have a large number of striae while those from Mozambique and Zululand have comparatively few.



Map 2. Western Indian Ocean showing distribution of *Ethalia carneolata* Melvill, 1897; each black triangle represents one or more records.

E. carneolata has previously been recorded from Mozambique as *E. striolata* (A. Adams, 1855) (Kilburn, 1977). Although the two are very similar in some respects, examination of type material reveals consistent differences in the form of callus deposition in the columella region (compare Figs 11 and 120). In the types of *E. striolata* from Borneo (BMNH 1968347, two syntypes, one here figured and designated lectotype, Figs 120–122), there are three distinct lobes of callus associated with the columella (hence Sowerby's name *trilobata* Sowerby in Reeve, 1875–8, now regarded as a synonym). In BMNH *E. carneolata* material, however, there are only two such lobes. All western Indian Ocean material examined by me has a two-lobed columella callus and is therefore referable to *E. carneolata*. An additional difference between the two taxa is that the thickened umbilical margin of *striolata* is distinctly and evenly spirally striate, while that of *carneolata* is at most weakly and unevenly striate. The variety *rubrostrigata* Melvill, 1904 (Figs 17–18), merely represents a rather striking colour variant and does not merit taxonomic recognition.

Melvill, in his original description, indicates his figures 25 & 26 (pl. 7) to represent *E. carneolata* and figure 24 to be *E. minolina*. Comparison of the figures with the type specimens, however, indicates fig. 26 to be *minolina* and fig. 24 to be his '*carneolata* var.' from the Persian Gulf.

The record of *striolata* from the Cocos Keeling Islands (Maes 1967) is incorrect; the figure given shows a specimen in which the columella callus is disjunct from the parietal lip. This is never the case in either *striolata* or *carneolata*. A more probable identification would be *Trochus lifuanus* Fischer, 1878, a species supposedly referable to *Talopena* (Iredale 1929).

Ethalia electra sp. n.

Figs 4f, 23–26.

Diagnosis: Spiral sculpture relatively strong, comprising primary and secondary elements; umbilicus with well defined, rather narrow funicle which ends as a small reflected notch near parietal end of columella; umbilical margin marked by thickened spiral cord; no obvious extra deposition of callus in columella region.

Description: Shell somewhat thin, depressed turbiniform, of moderate height (L/D = 0,71); teleoconch of nearly 5 whorls; whorls rounded, but somewhat shouldered, particularly early whorls; periphery at mid-whorl or nearly so; suture at periphery; base rounded. Sculpture relatively strong; spiral lirae develop on second whorl, third whorl with ±8 lirae; lirae becoming cord-like on fourth whorl; body whorl with *ca* 8 primary cords above periphery with secondary cords between these, and further lirae in intervals; cords roundly wedge-shaped in profile; base corded, but with narrower intervals and cords more flat-topped, ±13 cords between periphery and umbilical margin, with no obvious gradation in size. Axial sculpture of relatively coarse close-set collabral pliculae, particularly prominent on shoulder and in cord intervals, but often crossing cords; pliculae less obvious on base, except around umbilicus. Umbilicus open, of moderate width with a well developed, but narrow funicle $\frac{2}{3}$ of way up columella toward paries; end of funicle a reflected, concave notch in columella; umbilical margin

noticeably thickened, sculptured by spiral striae and close-set axial pliculae. Aperture subquadrate; little callus deposit on parietal lip; outer lip smooth or nearly so, strongly prosocline above periphery, orthocline below; interior nacreous.

Protoconch: Not examined under SEM, somewhat worn; diameter 180–200 μm.

Colour: Ground colour white to yellowish-white; apical surface washed with spiral bands of bright yellow and pale orange, shoulder with large brownish blotches, spiral cords flecked with white, yellow, orange and brown; base paler, but with larger, bolder flecks; umbilical margin surrounded with diffuse pinkish spots; umbilical funicle white.

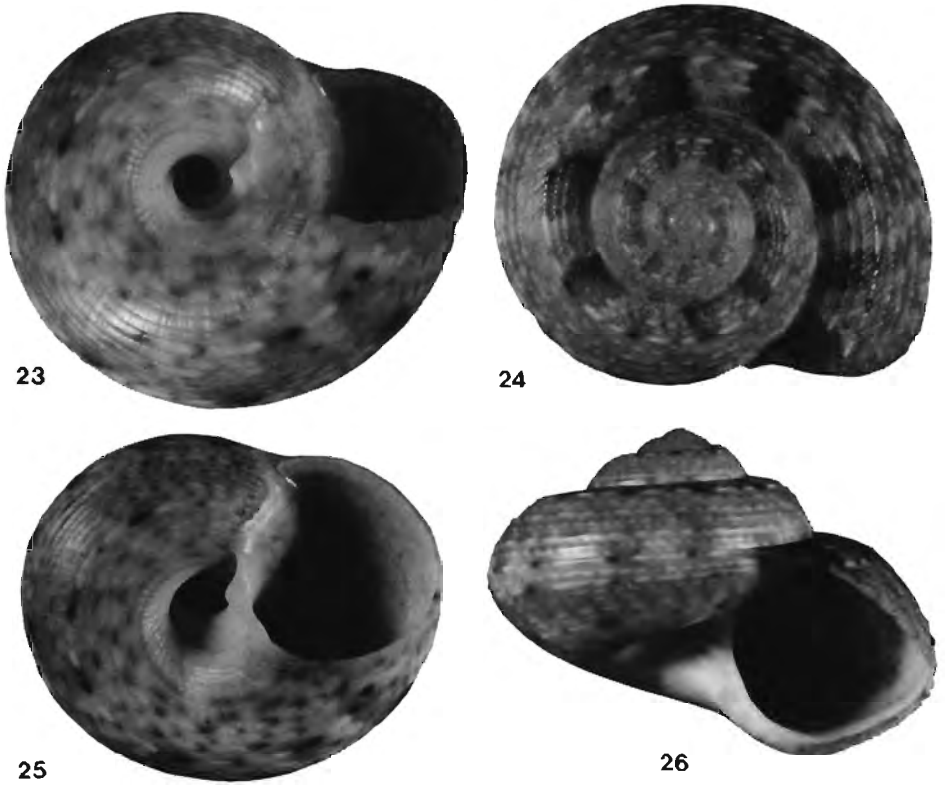
Dimensions: Holotype, diameter 9,3 mm, height 6,6 mm.

Radula and external anatomy: Unknown.

Distribution: Known only from the type locality.

Type material: Holotype, NMSA D9006/T246, off Kosi River mouth, Zululand (26°54,6′S:32°56,6′E), dead, 75 m, coral rubble, sandstone, marine growths, dredged NMDP.

Remarks: This species differs from other local species of *Ethalia* in its coarser spiral sculpture and much reduced callus deposit in the columella region. Of local



Figs 23–26. *Ethalia electra* sp. n., holotype, diameter 9,4 mm (NMSA D9006/T246).

species it is perhaps most similar to *Ethalia gilchristae* sp. n., but has a wider umbilicus and narrower, more sharply defined umbilical funicle, the termination of which is clearly disjunct from the paries.

Globally, this species most closely resembles species supposedly referable to *Talopena* Iredale, 1918, such as *lifuana* Fischer, 1878, from the Loyalty Islands and *gloriola* Iredale, 1929, from New South Wales (Fig. 131), particularly with regard to the disjunction between the umbilical funicle and the paries. It differs in being more depressed and in having a coarser sculpture. Comparison may also be made with *'Minolia' glaphyrella* Melvill & Standen, 1895 (13 syntypes, NMWC 1955.158.115–116, one here figured and designated lectotype, Fig. 135), likewise from the Loyalty Islands, but that species is smaller, more elevated and lacks the axial pliculation of *E. electra*.

In the absence of anatomical observations the generic position of this species cannot be confirmed. The form of the umbilicus is intermediate between that of *Monilea* and that of typical *Ethalia*. Although there is some similarity with *Talopena*, the type species of that genus (*incerta* Iredale, 1913) more closely resembles a *Monilea*, whilst the overall facies of *electra* is more reminiscent of an *Ethalia*. Consequently, until evidence to the contrary is provided, I have chosen to refer it to the latter genus.

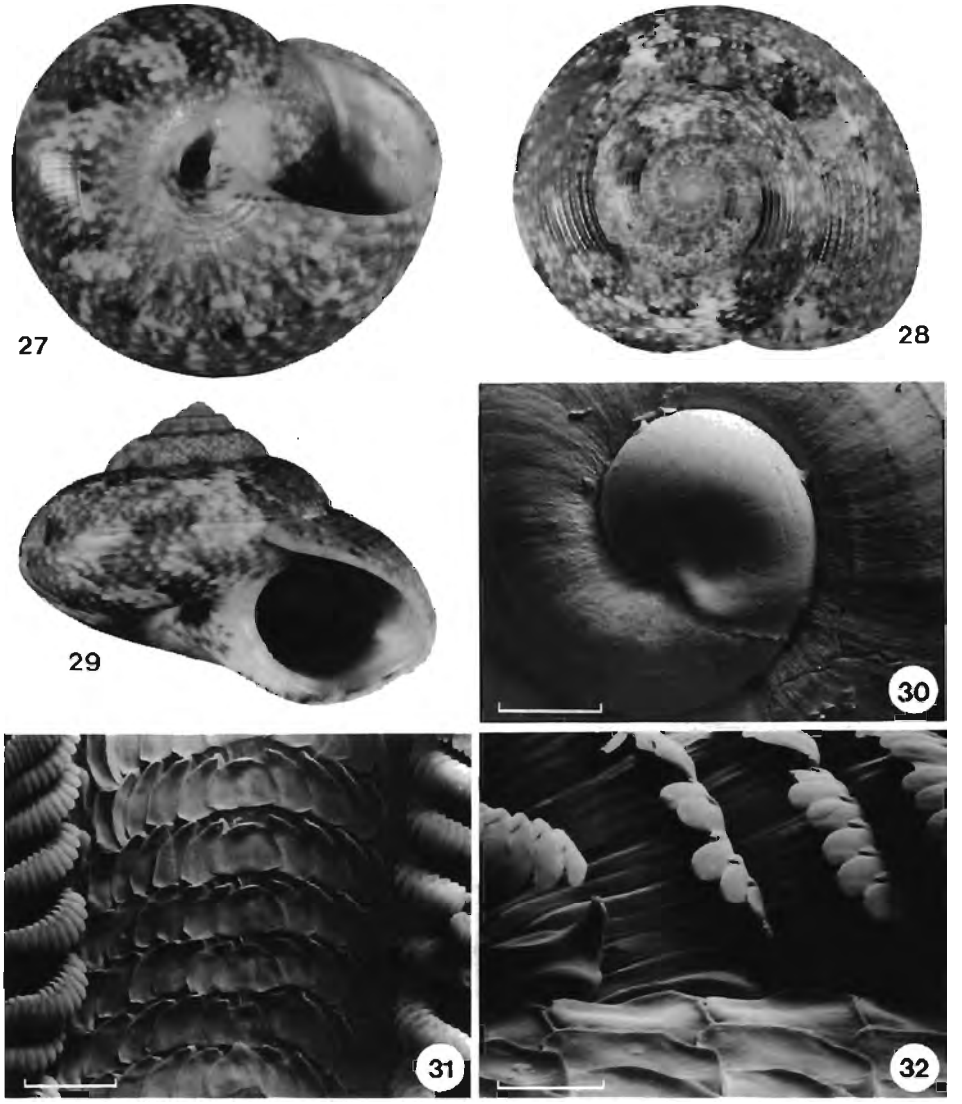
Etymology: Named after Electra, the 'bright one'; one of the Oceanides, daughters of Oceanus and Tethys.

Ethalia gilchristae sp. n.

Figs 1–2, 4c, 27–34; Map 3.

Diagnosis: Shell depressed turbiniform; apical surface lustreless, sculptured by numerous close-set spiral lirae with narrow intervals; base more glossy, sculptured by widely spaced incised spiral striae; umbilicus open, funicle present; callus deposit obscuring little of umbilicus, tending to be three-lobed.

Description: Shell depressed turbiniform (L/D = 0,66–0,74); teleoconch of up to 6 whorls; periphery round to roundly angular, at or just below mid whorl; suture level, early whorls often somewhat tabulate below suture. Apical surface lustreless, sculptured by numerous close-set, spiral lirae; lirae somewhat wedge-shaped in profile; intervals narrow, fine intermediary lirae may develop in intervals on body whorl; base more glossy, striate rather than lirate; striae fine, becoming progressively more widely spaced toward umbilicus. Axial sculpture of numerous collabral growth-lines, most obvious on apical surface and around umbilicus. Umbilicus open, width variable; margin thickened, but not clearly demarcated from base; spiral sculpture sometimes slightly stronger at umbilical margin; interior of umbilicus with well developed spiral funicle terminating in centre of columella. Aperture subquadrate; columella with callus deposit in three lobes (Figs 4c, 27), one corresponding with thickened umbilical margin, another with umbilical funicle and the third with the parietal callus; parietal callus white, concentrated at top of columella and spreading as a thin translucent layer over paries; inner edge of columella nacreous; outer lip smooth, strongly prosocline above periphery, orthocline or nearly so beneath; interior nacreous.



Figs 27–32. *Ethalia gilchristae* sp. n. 27–29, holotype, diameter 12,5 mm (NMSA E1684/T29); 30, protoconch, bar = 100 μm (paratype 18); 31, central field of radula, bar = 100 μm (*ex* paratype 1); 32, latero-marginal area of radula showing broad base and reduced cusp of first marginal (arrow), bar = 50 μm (*ex* paratype 1).

Protoconch (Fig. 30): Diameter 200–240 μm; apex rounded, but connected to terminal lip by well developed thickening; surface not obviously sculptured; terminal lip sinuous, a slight subterminal varix present.

Colour: Pattern very variable; specimens variously mottled with shades of white, yellow, orange, pink, red and brown, or a combination thereof, in blotches, spots, lines and flames. Some specimens very boldly marked, others of

a more uniform colour; colour pattern often following spiral sculpture, lirae usually variegated with white; umbilicus generally whitish with brown or reddish markings.

Dimensions: Holotype, diameter 12,5 mm, height 9,1 mm; largest specimen, diameter 13,4 mm, length 9,5 mm.

Operculum (Fig. 2): Corneous, thick, multispiral, but with relatively few whorls; nucleus central; no microscopic spiral lirae on exterior surface; overlap between whorls narrow, peripheral fringe not obviously radially striate.

Radula (Figs 31–32): Formula $\infty + (1) + 5 + 1 + 5 + (1) + \infty$, 70–80 transverse rows; rachidian and laterals with relatively well developed basal plates, but lacking cusps; rachidian triangular to semicircular, broader than long; inner laterals subtriangular, fifth lateral subquadrate, overlap simple. Marginals numerous with apices curled over; cusps spatulate, each with a prominent thumb-like denticle on its outer edge and a smaller one on the inner edge (usually hidden); first marginal a stout latero-marginal plate with reduced shaft and cusp (Fig. 32).

External anatomy (Figs 1, 33): Body yellowish-white with patches of white

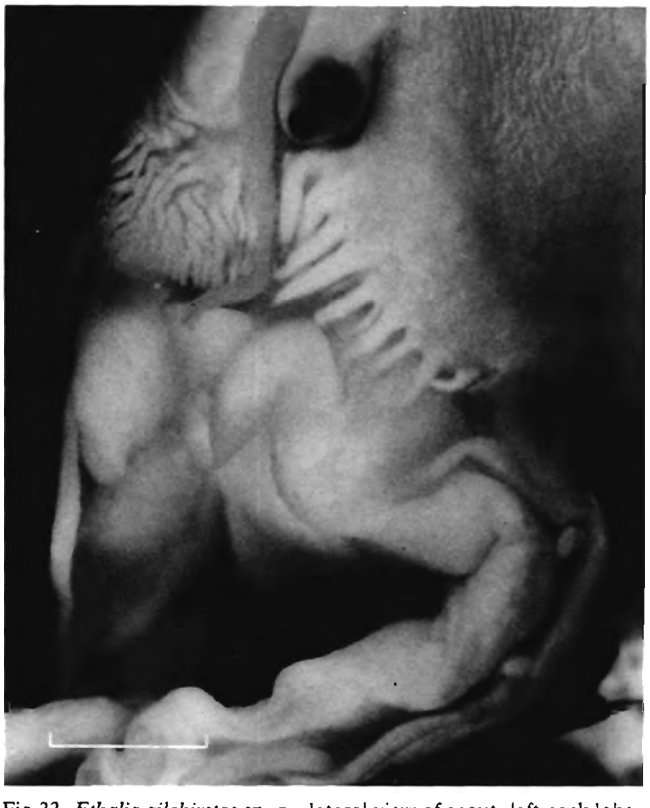


Fig.33. *Ethalia gilchirstae* sp. n., lateral view of snout, left neck lobe, foot and epipodium, preserved specimen, bar = 1,0 mm (NMSA D9222).

pigment, particularly on sides of foot; sole of foot sometimes mottled with pale brown; columella area and circum-opercular region usually stained red-brown. Cephalic tentacles of moderate size, micropapillate, sometimes banded with fine black rings, but more frequently not so; cephalic lappets absent, forehead relatively wide; eye stalks well developed but not noticeably elongate, terminally bulbous, not fused to cephalic tentacles; eye large, black; right post-optic tentacle absent. Snout relatively well developed, cylindrical, expanding slightly subterminally; distal 1/4–1/3 with long, finger-like papillae (Fig. 33); lips D-shaped, gently lobed, not papillate, split mid-ventrally. Left neck lobe a very low ridge with a series of *ca* 14 white, unbranched, finger-like projections (digits); digits frequently alternating in size and anterior ones larger than posterior ones (Fig. 33). Right neck lobe a broad undulating fold, rolled to form an exhalant siphon during life; margin smooth; not fused to eye stalk. Epipodial tentacles micropapillate, four on each side of body, arising from beneath epipodial fold; one immediately posterior to neck lobe, one level with anterior edge of operculum and two below operculum. Epipodial fold a low ridge, notched above bases of epipodial tentacles; fold continues beyond operculum and joins posteriorly in the mid-line. Epipodial sense organs well developed, stalked; one under each neck lobe and one associated with the base of each epipodial tentacle, occasionally two; sense organ at base of anterior tentacle on left lies just posterior to it, that at base of anterior tentacle on right is posteriorly displaced somewhat further; sense organs of other tentacles lie ventral to tentacle base. Foot truncated anteriorly, tapering to a point posteriorly; propodium indented medially and drawn out laterally in to lobes; foot constricted posterior to propodial lobes, but broadening to its maximum width just behind this; sides of foot not papillate.

Ctenidium (Fig. 34): Long, extending whole length of mantle cavity; afferent ctenidial membrane long, extending well beyond junction of transverse pallial vein and afferent ctenidial vessel, only the distal 1/4–1/5 of ctenidium remaining free; for the most part bipectinate, but proximal third (portion posterior to transverse pallial vein) monopectinate; filaments elongate rather than triangular, with prominent bursicles and expanded tips; filaments on left of ctenidial axis somewhat reduced.

Distribution: South western Indian Ocean; currently known only from Zululand and Réunion Island; depth range 45–225 m, but southern African material has not been found deeper than 100 m; living specimens 49–70 m; mixed substrata, usually sandy.

Type material (all dredged NMDP): Holotype, NMSA E1684/T29, S.E. of Kosi River mouth, Zululand (26°55,3′S:32°55,4′E), 50 m, medium sand, rubble; paratypes, 1–3, NMSA D8939/T30, living, data as holotype; paratypes 4–9, NMSA D6184/T31, do, living, 50 m, medium sand, algae; paratypes 10–12, NMSA E1686/T32, data as paratypes 4–9; paratypes 13–17, NMSA D7375/T33, off Boteler Point, Zululand, living, 70 m, some coarse sand, some shell rubble; paratypes 18–28, NMSA D6884/T34, off Kosi River mouth, Zululand, living, 50 m, medium sand, algae; paratypes, 29–33, NMSA D6181/T35, S.E. of Kosi River mouth, Zululand, living, 50 m, medium sand, algae; paratypes 34–37, NMSA D8440/T36,

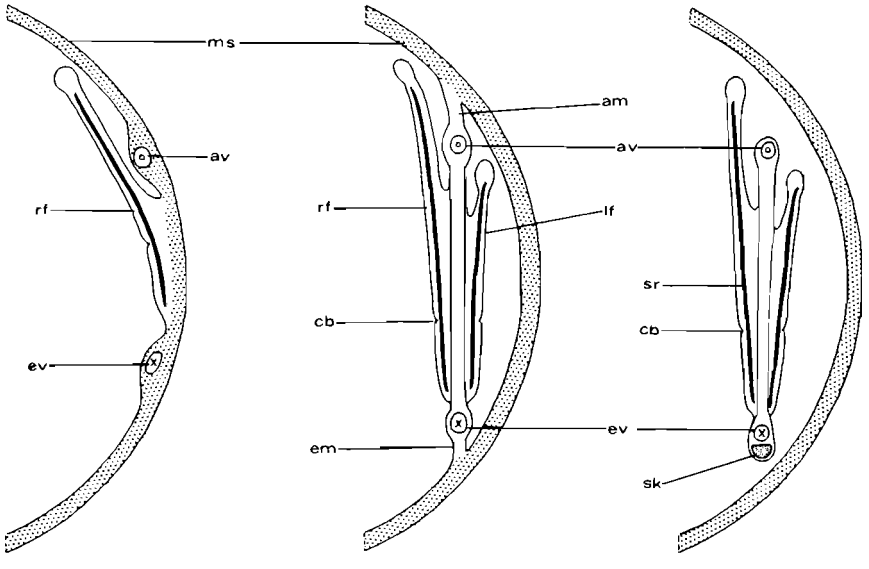


Fig. 34 *Ethalia gilchristae* sp. n., diagrammatic representation of transverse sections through the ctenidium and mantle skirt, viewed from the anterior; A, in the region posterior to the junction of the transverse pallial vein and the afferent ctenidial vessel, where the ctenidium is monopectinate; B, through the middle portion of the ctenidium, anterior to the junction of the transverse pallial vein and the afferent ctenidial vessel, where filaments are present on both sides of the ctenidial axis; C, through the distal portion of the ctenidium which lies free within the mantle cavity, not attached to the mantle skirt. am, afferent ctenidial membrane; av, afferent ctenidial vessel; cb, ctenidial bursicle; em, efferent ctenidial membrane; ev, efferent ctenidial vessel; lf, left ctenidial filament; ms, mantle skirt; rf, right ctenidial filament; sk, skeletal rod supporting ctenidial axis; sr, skeletal rod supporting ctenidial filament.

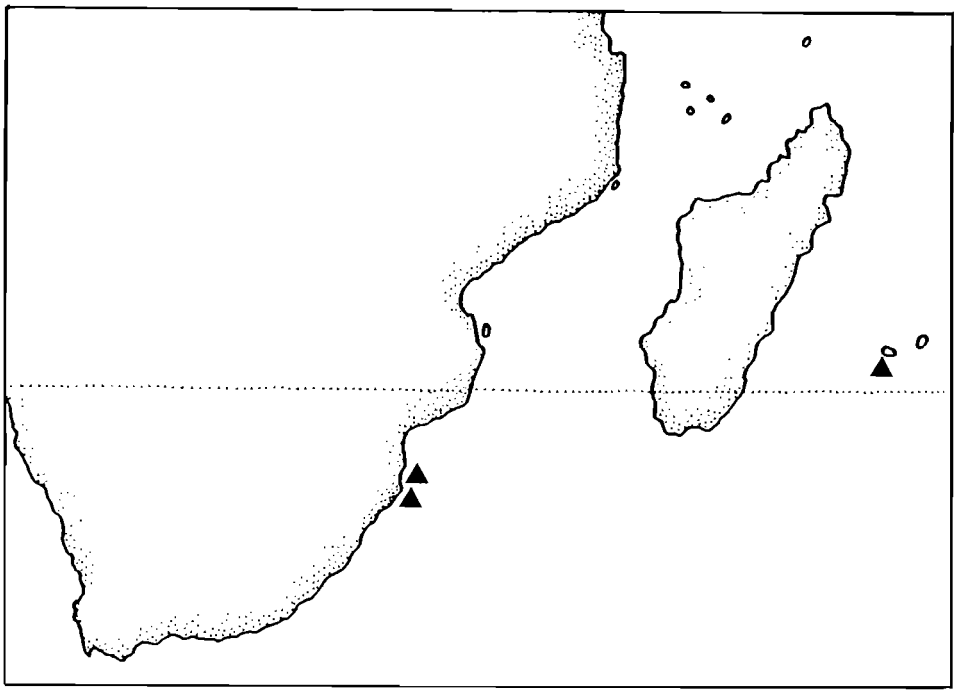
off Jesser Point, Zululand, 70 m, medium sand; paratypes 38,39, NMSA D6328/T37, S.E. of Kosi River mouth, Zululand, 45–47 m, red algae, sponges; paratype 40, NMSA D7559/T38, off Hully Point, Zululand, 50 m, fine sand.

Additional regional locality data (all NMSA, dredged NMDP, dead, unless indicated otherwise): ZULULAND: N.E. of Kosi Bay, 51–53 m, coarse sand (S4959); off Kosi River mouth, 50 m, (D7923); do, living, 51 m, sand, stones and large algae (S4016); S.E. of Kosi River mouth, 45 m, sand, stones and large algae, (S4825); do, 50 m, fine, slightly muddy sand (E1756); do, living, 50 m, coral slabs (S4012); do, 65 m, sponge, gorgonians, medium sand (D8045); off Boteler Point, 66 m, sand, rocks (S3840); do, living, 70 m, coral rubble (D6380); do, 78 m, coarse sand (D7531); do, living, 50 m, dead coral rubble, *Lithothamnion* (D7467); off Dog Point, living, 70 m, sandstone conglomerate (D6479); off Island Rock, 62 m, sandstone, coral, marine growths (E2923); off Jesser Point, 48–58 m, sand, shell rubble (D6531); do, 54 m, medium sand (E816); off Sodwana Bay, living, 49–53 m, sand (S4741); do, living, 50 m, *ex* CSIR Water Research (B4200); do, living, 58 m, coral rubble (S5113); do, living, 61 m, sand (S3872); do, living, 70 m, coral rubble (S3920); do, 70 m, dead coral rubble (S4524); do, 77 m, dead coral (S4769);

Sodwana Bay, *ex* CSIR Water Research, no depth given (D4920, D4362); N.E. of Liefeldt's Rocks, 50 m, *Lithothamnion*, medium sand, dead coral rubble (E4261); off Liefeldt's Rocks, living, 50 m, *Lithothamnion*, stones, some coarse sand (E4340); off Gipsy Hill, 65–70 m, broken shell (E3577, E7467); off Leadsman Shoal, 100 m, dredged A. Connell (B4048); off Cape Vidal, 75–80 m, broken shell (E4472).

Extralimital locality data: RÉUNION ISLAND: 21°05'S:55°12'E, 170–225 m, dredged R. V. *Marion-Dufresne* cruise 32, 1982, st. DC56 (MNHN).

Remarks: A beautiful species which exhibits considerable similarity to *E. minolina* Melvill, 1897, from the Persian Gulf (holotype, BMNH 1897.7.30.108, Figs 125–127), particularly in the form of the columella callus (compare Figs 4c and 4d); however, *minolina* has more close-set spiral striae on the adapical surface and these also occur on the base. *E. minolina* var. *infralaevior* Schepman, 1908, from Indonesia, has the fine spiral sculpture of *minolina* on the apical surface, but is almost totally smooth basally. Schepman's figured specimen came from *Siboga* station 37 and is here refigured (Figs 128–130) and designated varietal lectotype (ZMAN). The other specimen in this type lot is juvenile, but has distinct spiral striae on the base and is almost certainly a different species. *Trochus (Solariella) lamprus* Watson, 1880 (holotype, BMNH 1887.2.9.291), from shallow water off Fiji (Figs 123–124), clearly belongs to this group and may well prove to be an earlier name for Schepman's *infralaevior*, but there is insufficient material available at



Map 3. South-western Indian Ocean showing distribution of *Ethalia gilchristae* sp. n.; each black triangle represents one or more records.

present to assess intraspecific variation. Also similar in respect of umbilical form is '*Monilea' philippii* A. Adams, 1855, from 'China Seas', but that species is higher (L/D = 0,78) and has coarser spiral sculpture (see Appendix and Figs 109–110).

E. gilchristae differs from *E. carneolata* Melvill, 1897, in possessing more rounded whorls, its greater development of spiral sculpture and in the form of the columella callus (compare Figs 4a and 4c). The most similar local species is *E. bysma* sp. n., but that species has numerous fine spiral striae on the base and its umbilicus is almost closed by the funicular callus (Fig. 4e).

Species supposedly referable to *Talopena* Iredale, 1918, such as *lifuana* Fischer, 1878 and *gloriola* Iredale, 1929 (Fig. 131), differ from *E. gilchristae* in having no extra callus deposition at the columella/parietal junction and thus the umbilical funicle remains disjunct from the paries. The variable width of the umbilicus in the present species does not appear to be linked with sex (cf. Lindberg & Dobberteen 1981).

Etymology: This species is named for Dr Barbara M. Gilchrist, friend and mentor during my student days at Bedford College, London University.

Genus *Ethminolia* Iredale, 1924

Ethminolia Iredale, 1924: 228, type species (monotypy) *Ethminolia probabilis* Iredale, 1924.

Sericominolia Kuroda & Habe, 1952: 85; Kuroda & Habe, 1954: 84(92), fig. 1 (radula); Kuroda, Habe & Oyama, 1971: 42 (synonym of *Ethminolia*), type species (o. d.) *Minolia stearnsii* Pilsbry, 1895.

?Conotalopia Iredale, 1929: 271, type species *Minolia henniana* Melvill, 1891.

Diagnosis: Shell depressed, trochoid-turbiniform to turbiniform, often thin; whorls frequently shouldered; umbilicus open, lacking callus deposition; protoconch with well developed apical beak; radula like that of *Ethalia* but shorter (<60 transverse rows); external anatomy unspecialised, with distinct forehead between cephalic tentacles and unbranched left neck lobe digits; ctenidium bipectinate for most of its length, terminal portion free; operculum lacking microscopic spiral lirae.

Radula: Formula $\infty + (1) + 5 + 1 + 5 + (1) + \infty$. The radula of the type species has not been described or figured. That of an unidentified species from Hong Kong and of *E. vitiliginea* have been figured by Hickman (1985: pl. 1a, b) and Hickman & McLean (1990: fig. 85a, g) respectively. That of *E. stearnsii* is described below and figured (Figs 66–67); all are very similar. There is clearly a resemblance to that of *Ethalia*, particularly with regard to the retention of well defined base plates on the rachidian and lateral teeth, the presence of a subtriangular, weakly cusped latero-marginal plate and the spatulate shape of the cusps on the marginals. It is evidently shorter than that of *Ethalia* (40–45 transverse rows in *E. vitiliginea* (personal observation) and 30–35 in *E. sculpta*), but this may be at least partly a function of the size of the species concerned. That these observations are typical of the genus, however, needs confirmation.

External anatomy (Fig. 35): No data are available concerning the external anatomy of the type species. That of *E. stearnsii* (described below) resembles that of the *Ethminolia* sp. described by Hickman (1985). It is very similar to *Ethalia* except that the left neck lobe in that genus consists almost entirely of finger-like

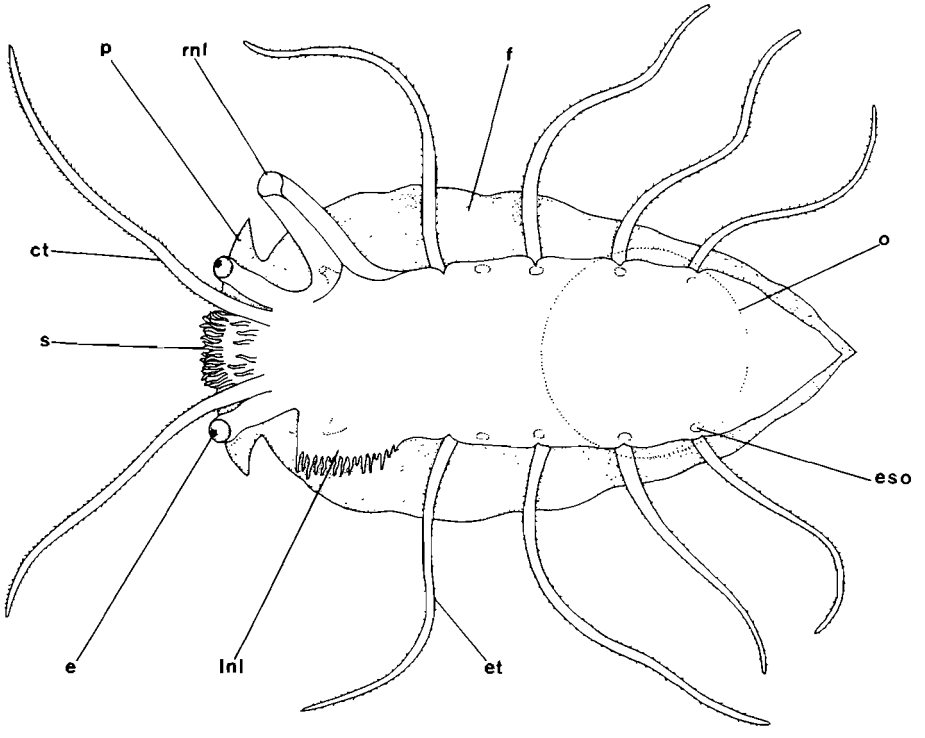


Fig. 35. *Ethminolia stearnsii* (Pilsbry, 1895). Diagrammatic representation of external anatomy: ct, cephalic tentacle; e, eye; eso, epipodial sense organ; et, epipodial tentacle; f, foot; lnl, left neck lobe; o, operculum; p, propodium; rnl, right neck lobe; s, snout.

digitations. In *Ethminolia* the digitations are smaller and are borne on a distinct lobe of tissue.

Operculum: I have examined the opercula of *Ethminolia sculpta*, *E. stearnsii* and *E. vitiliginea*. All lack microscopic spiral lirae and are similar to that described for *Ethalia*, although the peripheral fringe usually has distinct radial striations.

Remarks: Iredale's description of this genus is more or less useless as it gives no diagnostic features. In the absence of information regarding the radula and soft parts of the type species, the genus still remains inadequately defined and its utilisation is thus subjective. Persistent attempts to obtain preserved live-taken material of *E. probabilis* have failed.

Ethminolia is used here *sensu lato* as a taxon of convenience for a somewhat variable group of umboniine species which, at present, cannot be placed with certainty in any other genus group taxon. The most typical local species in terms of shell morphology is *Ethminolia durbanensis* (Kilburn, 1977), but for the purposes of this revision I have also included species of considerably larger size and species with much coarser sculpture. The generic placement of some of these species may need to be changed when more information and preserved specimens become available.

Kuroda & Habe (1952) proposed *Sericominolia* (type species *Minolia stearnsii*

Pilsbry, 1895), but neither gave reasons for this nor a description of the taxon. Later, Kuroda, Habe & Oyama (1971) synonymised it with *Ethminolia*. In fact, *E. stearnsii* is one of a small group of rather atypical and poorly known *Ethminolia* species, including *E. vitiliginea* (Menke, 1843) from southern Australia, and *E. eilikrines* (Melvill, 1891), from the Philippines (Figs 132 and 133, respectively). These generally have larger, more elevated and thinner shells than is typical for *Ethminolia* and have a poorly developed apical beak on the protoconch (like that of *Ethalia*). *'Monilea' vernicosa* Gould, 1861, from southern Japan and the Philippines (Fig. 136) is also similar, but may be distinguished by its umbilical funicle (although I have seen specimens of *E. vitiliginea* with a rudimentary funicle). *M. vernicosa* is intermediate between the *stearnsii* group and *'Talopena' gloriola* Iredale, 1929, which has a well developed umbilical funicle and which, in turn, is somewhat reminiscent of an *Ethalia*.

The systematic relationships of this group of umboniines seem particularly complex and the problem is exacerbated by the lack of anatomical data. In terms of shell morphology there appears to be a graded series ranging from small relatively strongly sculptured forms (*E. sculpta*) through small, weakly sculptured forms (*Ethminolia s.s.*), to larger, thin shelled species lacking an umbilical funicle (*E. stearnsii*), and large, thin-shelled species with a umbilical funicle (*E. vitiliginea* (some specimens), *E. vernicosa* and *'Talopena' gloriola* – in ascending order of funicular development), ending with species here referred to *Ethalia* in which the shell is thicker and which have a well developed funicle with at least some degree of callus deposition around the umbilicus. With a graded series such as this, defining the limits of genera becomes extremely difficult, clearly characters in addition to shell morphology must be considered.

Conotalopia Iredale, 1929, another of Iredale's unsupported nomenclatural proposals, needs to be investigated as a possible synonym of *Ethminolia*. In terms of shell morphology the type species, *Minolia henniana* Melvill, 1891, from Queensland, simply looks like a square-set version of *E. probabilis*. *Antisolarium* Finlay, 1926, is somewhat similar to *Ethminolia*, but the animal has a reduced forehead, a snout which projects from under cephalic tentacles, a radula with multidenticulate cusps on the marginal teeth and a monopectinate ctenidium (personal observation) – features which place it with the more advanced umboniines in the tribe Umboniini.

Key to species of *Ethminolia* in southern Africa and Mozambique.

1 Shell with three keel-like spiral angulations 2
– Shell lacking keel-like angulations; angulation, if present, only at shoulder 4

2 Apex coloured, pink to deep maroon 3
– Apex not differentially coloured ..... **nektonica**

3 Base lirate throughout; apical surface sculptured by spiral keels and axial ribs ..... **sculpta**
– Base lacking strong liration, for the most part smooth; sculpture generally weak, at most slight spiral angulation and weak subsutural crenulation ..... **gravieri** (in part)

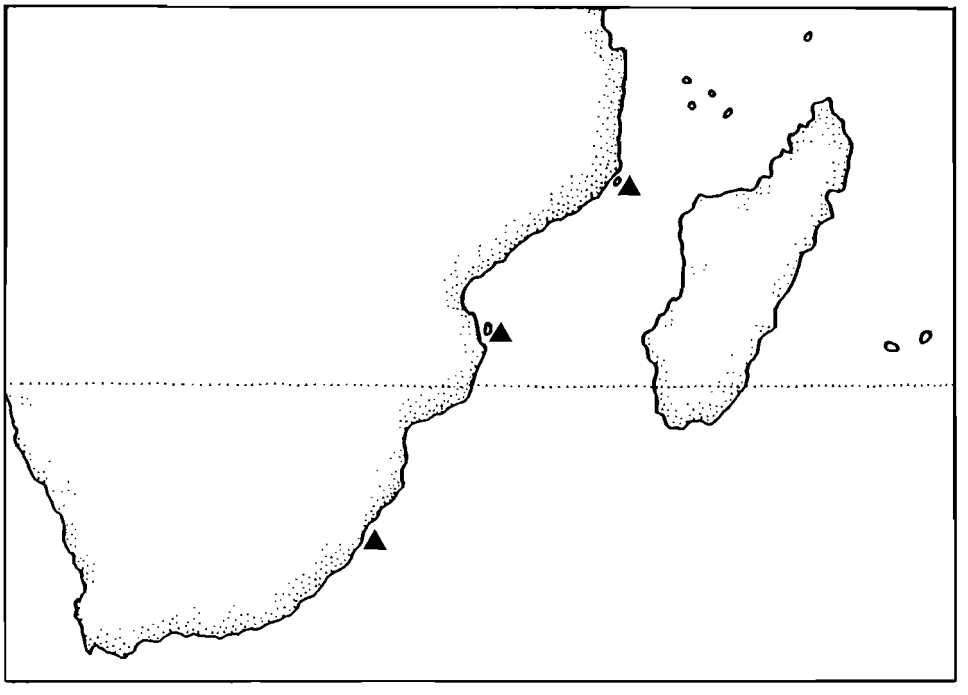
4 Apex pink-maroon; spiral sculpture almost totally lacking ..... **gravieri** (in part)
– Apex usually pale (whitish), rarely pink-maroon; spiral lirae or striae present 5
5 Shell thin and fragile, relatively large (diameter frequently >7,0 mm), whorls lacking distinct shoulder; spiral sculpture more or less even throughout, comprising fine close-set spiral lirae; lirae much wider than their intervals, in excess of ten lirae above periphery on body whorl **stearnsii**
– Shell more solid, smaller (diameter rarely exceeding 5,0 mm), whorls shouldered; adapical surface sculptured by raised spiral lirae, intervals between lirae wider than lirae themselves, less than ten lirae above periphery on body whorl; base somewhat more weakly sculptured than adapical surface ..... **durbanensis**

Ethminolia durbanensis (Kilburn, 1977) **comb. n.**

Figs 36–39; Map 4.

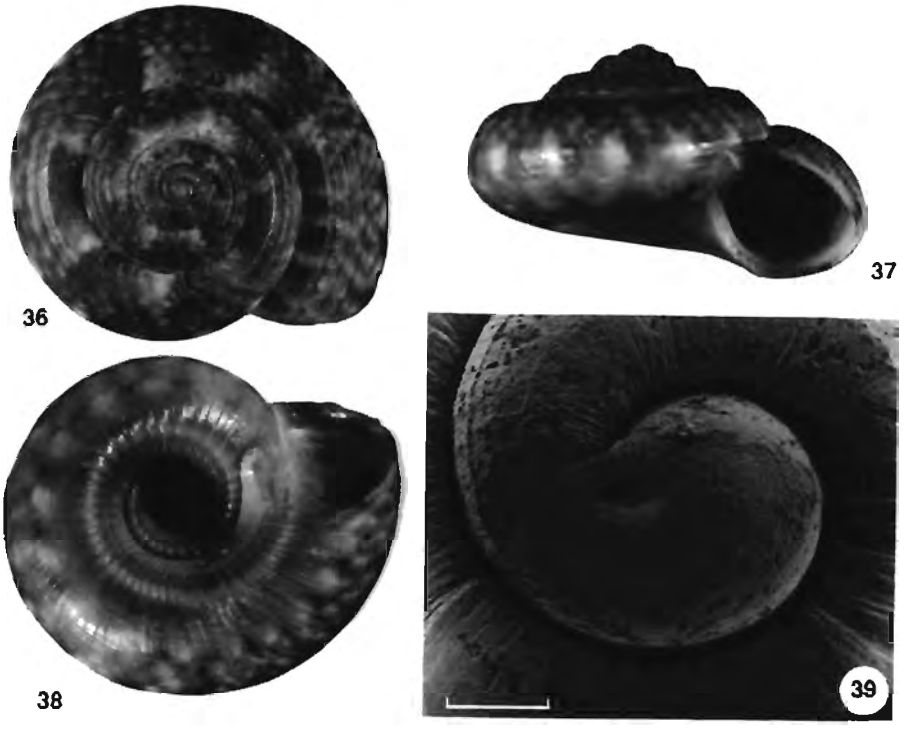
Solariella durbanensis Kilburn, 1977: 177, figs 6–8. Type loc.: Durban Bay, shallow-water dredgings.

Notes: Little needs to be added to Kilburn's original description. The species shows much greater affinity to umboniine species than to the Solariellinae. This is confirmed by examination of the protoconch (Fig. 39) which is small (diameter



Map 4. South-western Indian Ocean showing distribution of *Ethminolia durbanensis* (Kilburn, 1977); each black triangle represents one or more records.

±200 μm) and typically umboniine. No living specimens have been obtained and the radula and external anatomy are therefore unknown. Considerable similarity in terms of shell morphology exists with the type species of *Ethminolia* (*E. probabilis* Iredale, 1924, from New South Wales), and for this reason I refer the species to that genus. *E. probabilis*, however, is larger with more sharply angled whorls, finer spiral lirae and the umbilicus is never as strongly sculptured. The most similar local species and one which commonly occurs with the present species is *E. sculpta* (Sowerby, 1897). That, however, has stronger spiral cords and coarse axial sculpture.



Figs 36–39. *Ethminolia durbanensis* (Kilburn, 1977). 36–38, holotype of *Solariella durbanensis* Kilburn, 1977, diameter 5,1 mm (NMSA A5040/T2045); 39, protoconch, bar = 50 μm (NMSA B8696).

Although previously known only from Durban Bay, the distribution is here shown to extend to northern Mozambique. The species appears to inhabit warm lagoonal environments.

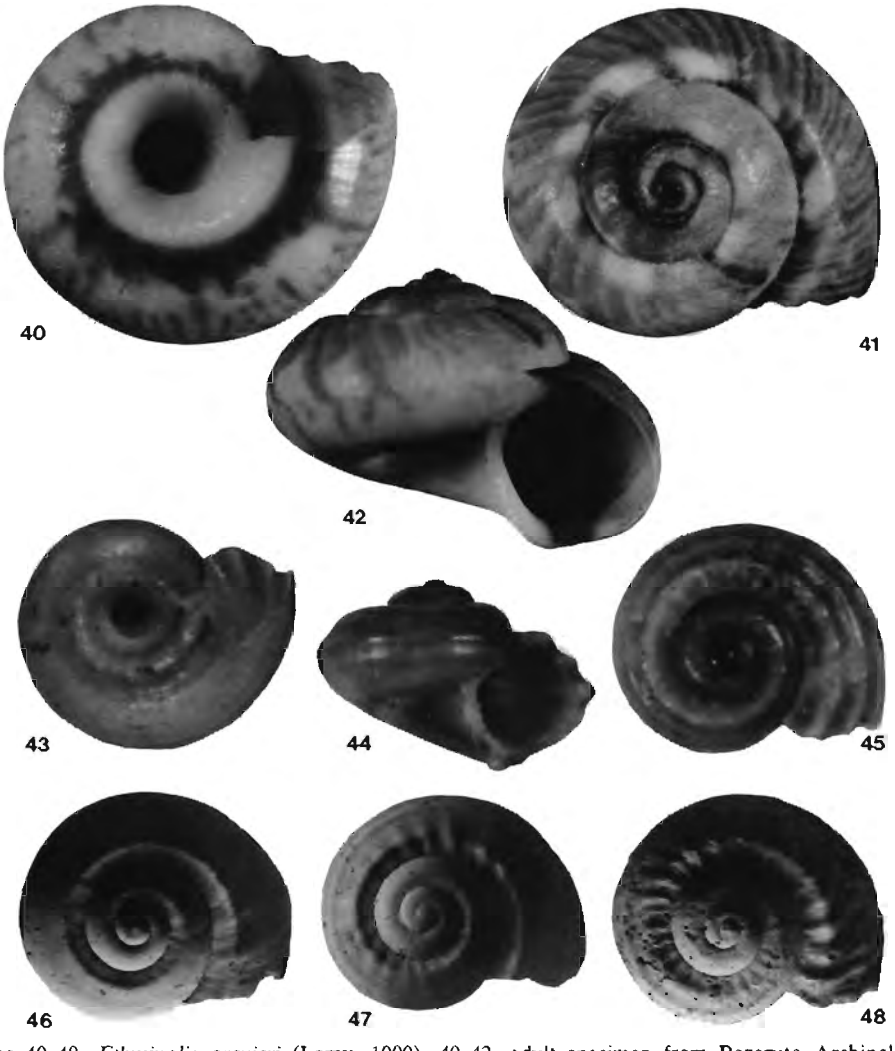
Additional locality data (all NMSA): NORTHERN MOZAMBIQUE: Nacala, dredged 5,5–18,5 m, F. Steiner (F8677); Mozambique Is., beach drift, R. Kilburn (K3160). SOUTHERN MOZAMBIQUE: North of Benguerua Is., Bazaruto Archipelago, dredged ±12 m, (G4466); north bay, Benguerua Is., Bazaruto Archipelago, R. Kilburn, (K320, K2252); Inhaca Is., R. & E. Kilburn (7081).

Ethminolia gravieri (Lamy, 1909) **comb. n.**

Figs 40–50; Map 5.

Cyclostrema gravieri Lamy, 1909*a*: 370; 1909*b*: 329, pl. 15, figs 1–3. Type loc.: 'sur la côte de Tuléar', Madagascar.

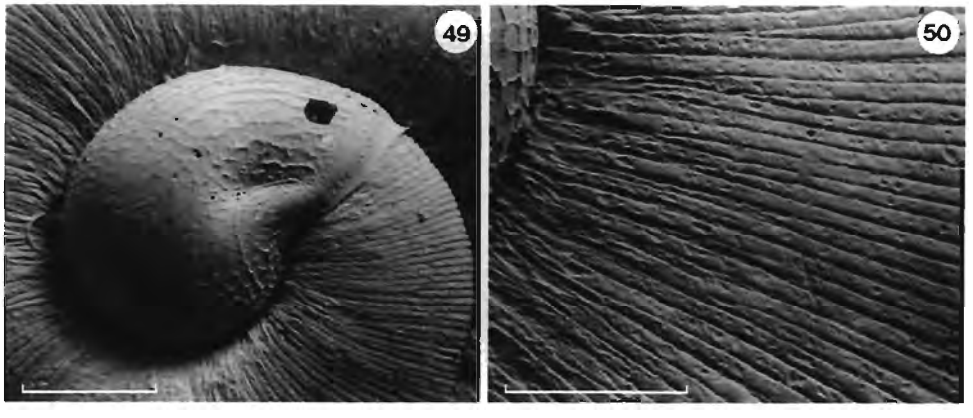
Diagnosis: Shell small, thin, depressed; white to dark red or maroon, commonly variably patterned in shades of maroon-pink; whorls rounded, usually with a distinct shoulder; sculpture generally obsolete, but some specimens with spiral cords and a pliculate umbilical margin; interior not obviously nacreous.



Figs 40–48. *Ethminolia gravieri* (Lamy, 1909). 40–42, adult specimen from Bazaruto Archipelago (NMSA K3145), diameter 4,1 mm; 43–45, holotype of *Cyclostrema gravieri* Lamy, 1909, diameter 1,3 mm (MNHN); 46–48, three juvenile specimens showing variation in development of sculpture, Bazaruto Archipelago, diameters 1,83 mm, 1,78 mm, 1,94 mm respectively (NMSA K3148).

Description: Shell small, thin, depressed trochoid-turbiniform (L/D = 0,68–0,82); teleoconch of up to 4,5 whorls; whorls rounded, usually with a tabulate shoulder, but shoulder sometimes weak or obsolete; periphery rounded, at or near mid-whorl; suture at mid-whorl, level or slightly sunken. Sculpture variable; most specimens lacking obvious spiral sculpture, but some with a distinct spiral cord at the shoulder angle, and two weaker ones, one at periphery and another between this and the shoulder; spiral sculpture when present usually strongest on early whorls; all specimens with an axial sculpture of microscopic collabral scratch-like lines (only visible under SEM, see Fig. 50), spirally corded specimens may also show some pliculation of shoulder caused by the development of weak axial ribs. Umbilicus open, margin rounded in smooth specimens, but often angled and pliculate in juveniles and spirally corded specimens. Aperture subcircular to quadrate; outer lip smooth; basal lip evenly rounded except when umbilical margin angled; columella lip concave, lacking callus deposit; parietal lip flat or slightly convex; interior not obviously nacreous.

Protoconch (Fig. 49): Typically umboniine with relatively strong reticulate sculpture; reticulation for the most part subhexagonal, but becoming spirally aligned towards terminal varix; dark to very dark red (deep maroon); diameter 180–200 μm.



Figs 49–50. *Ethminolia gravieri* (Lamy, 1909). 49, protoconch, bar = 75 μm; 50, scratch-like axial microsculpture, bar = 50 μm (NMSA K1089).

Colour: Ground colour white or nearly so, some specimens lightly suffused with pink others mostly purplish-red, many of an intermediate shade; often a spiral band of deep pink to maroon at the suture and around and/or in the umbilicus.

Dimensions: Holotype, diameter 1,3 mm, length 0,9 mm; largest specimen, diameter 4,8 mm, length 3,3 mm.

Radula and external anatomy: Unknown.

Distribution: Known only from the type locality (Tuléar, Madagascar) and the Bazaruto Archipelago in southern Mozambique, beach-drift to 15 m.

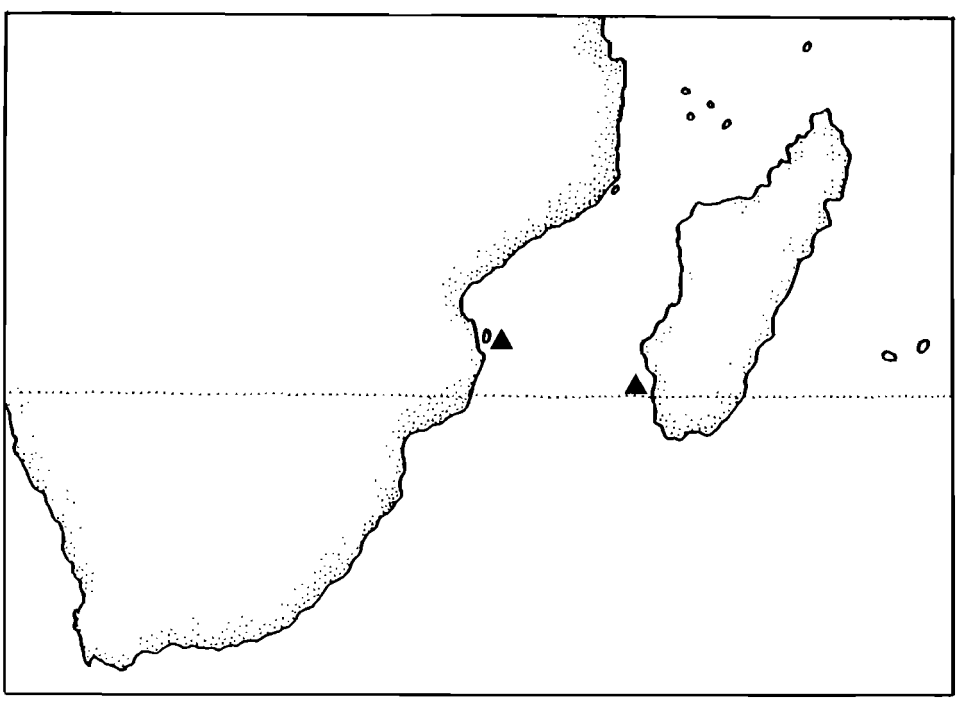
Type material: Holotype in MNHN, no catalogue number.

Additional locality data (all NMSA, dead): MOZAMBIQUE: Santa Carolina Is., R. Kilburn (F8679, K1809, K3148, K3158); do, sandbank between island and mainland (K339); between Bazaruto and Benguerua Is., dredged 3–12 m, R. Kilburn & E. Roscoe (K2673, K3147, K4258); Benguerua Is., north bay, (K1810); Magaruque Is., west bay, E. Roscoe (G2623, K1803, K3145, K3146).

Remarks: This species does not seem to have been reported subsequent to its original description. Unfortunately Lamy's holotype is very juvenile, comprising only 2,5 teleoconch whorls, and no further Malagasy material has been available to me. (J. Drivas of Réunion Island has not found the species on recent visits to the type locality – personal communication). The above description is thus based on Mozambican material.

It is with some hesitation that I have identified this material as Lamy's species. Most specimens from Mozambique lack the obvious spiral sculpture of the holotype, but some do possess distinct traces of spiral cording, particularly on the early whorls, suggesting a gradation in this character. In the absence of comparative adult material from Madagascar I can conclude only that a single species is involved.

E. gravieri can be confused with no other local species on account of its small size and coloration, particularly the dark purplish-red apex. *E. sculpta* (Sowerby,



Map 5. South-western Indian Ocean showing distribution of *Ethminolia gravieri* (Lamy, 1909); each black triangle represents one or more records.

1897), also has a reddish apex, but in that species the colour is usually restricted to the protoconch and the shell as a whole is much more coarsely sculptured with well defined spiral lirae on the base. Some similarity exists with *Isanda hornungi* (Bisacchi, 1931) from the Red Sea, but the type specimens of that species are more elevated, thicker shelled and have a narrower umbilicus (MCSN, three syntypes).

It is possible that *E. gravieri* may eventually prove to belong to *Isanda* H. & A. Adams, 1854, but with neither details of radula form for *gravieri* nor an adequate definition of *Isanda*, I prefer to place it in *Ethminolia*.

Ethminolia nektonica (Okutani, 1961)

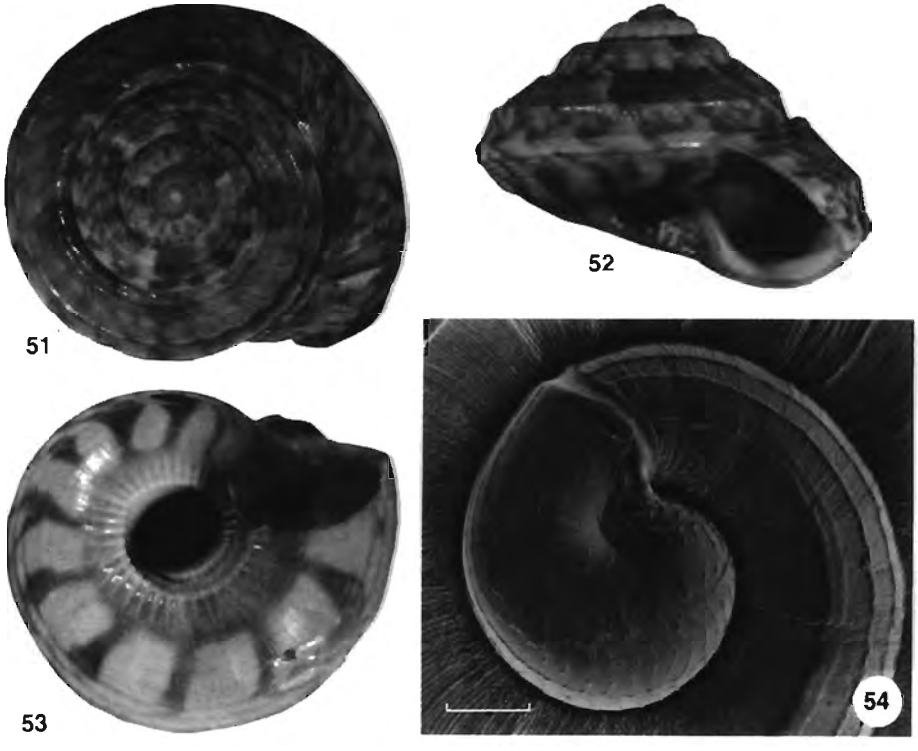
Figs 51–54; Map 6.

Solariella nektonica Okutani, 1961: 304, figs 1–8. Type loc.: off Kushikino, Kyushu, Japan (31°35,3'N:130°06,5'E), 89 m.

Solariella nektonica tajimensis Okutani & Sakurai, 1968: 71, fig. 1. Type loc.: off Kasumi, Japan Sea side of Hyogo Prefecture, Honshu, Japan, 35 m.

Ethminolia nektonica; Tsuchida & Kitao, 1987: 259, figs 1, 3, pl. 1, figs 1–9.

A small number of specimens closely resembling *E. nektonica tajimensis* have been dredged off Réunion Island and Zululand, none alive. This species has not



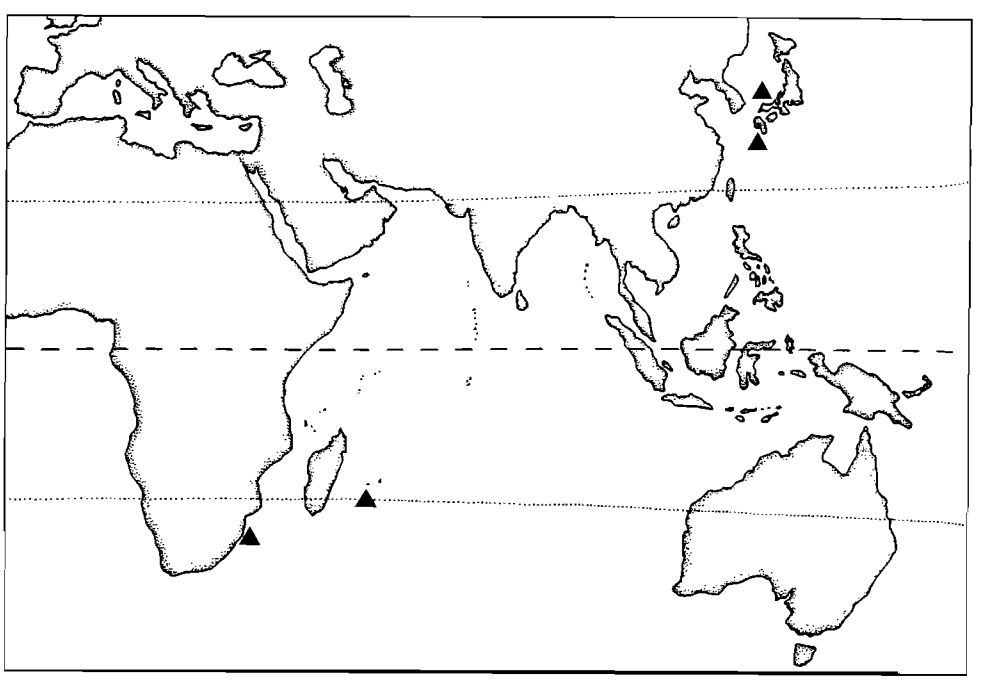
Figs 51–54. *Ethminolia nektonica* (Okutani, 1961). 51, apical view, diameter 6,0 mm (NMSA S1138); 52, apertural view, diameter 5,8 mm (NMSA S1138); 53, basal view, diameter 4,5 mm (NMSA E3548); 54, protoconch, bar = 50 μm (MNHN, Réunion Is.).

previously been recorded outside Japanese waters. Réunion Island material is somewhat smaller than that from Japan or southern Africa.

Tsuchida & Kitao (1987) pointed out the umboniine rather than solarielline affinities of the species and figured the radula. The size and shape of the protoconch are also umboniine rather than solarielline (Fig. 54). The relationships of *E. nektonica* within the Umboniinae, however, need to be studied further. The shape of the shell is somewhat intermediate between *Ethminolia* and *Pseudominolia*, but Okutani's original drawings of the living animal are not sufficiently detailed to permit further comment. The broad multidenticulate cusps of the inner marginal teeth of the radula may perhaps indicate a closer relationship with *Pseudominolia*. However, in the absence of further evidence to support this, I follow Tsuchida & Kitao (1987) in referring the species to *Ethminolia*.

The species is superficially similar to *Ethminolia impressa* (G. & H. Nevill, 1869) [= *Minolia eucoronata* Sowerby, 1905, see Appendix], but that species is smaller, lacks a keel-like spiral cord between the shoulder and the periphery and has a more coarsely pliculate umbilical margin.

E. nektonica is very similar to *'Solariella' illustris* Sturany, 1903, described from the Red Sea and it is possible that the latter could represent a deep-water, Erythraean subspecies of *nektonica*. It is larger (diameter up to 9,0 mm, compared to 7,2 mm for *nektonica*), more elevated (L/D up to 0,75 compared to 0,65), has less strongly keeled whorls and a more finely crenulate umbilical margin. There are also



Map 6. Indian Ocean and western Pacific Ocean showing distribution of *Ethminolia nektonica* (Okutani, 1961); each black triangle represents one or more records.

differences in the colour pattern, particularly on the base. This taxon is currently being studied by R. Janssen of the Senckenberg Museum.

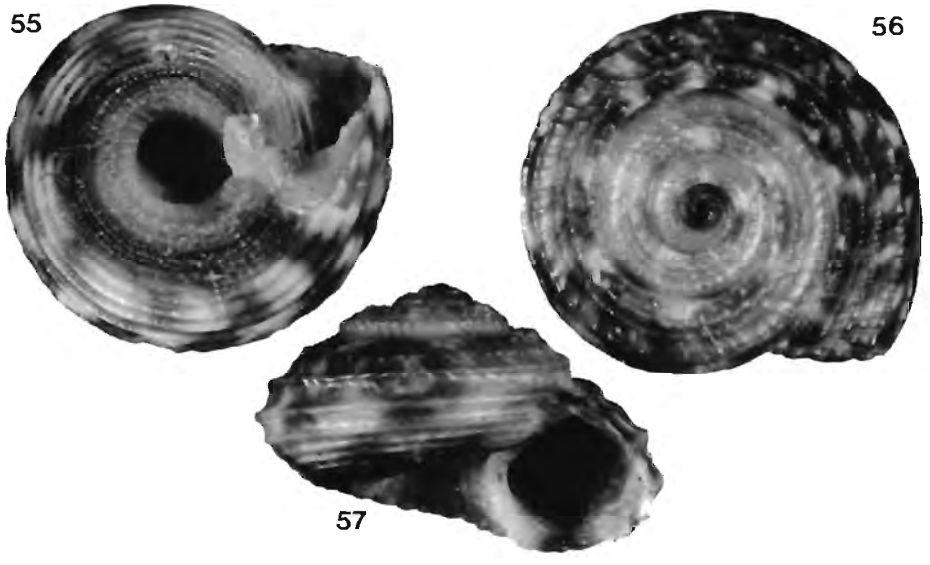
Regional locality data: ZULULAND (all NMSA, dredged NMDP, dead): off Lala Neck, 74 m, shell and sand (S3486); off Gipsy Hill, 63–70 m, sandstone rocks, sand and marine growths (S3473); N.E. of Leven Point, 250 m, coarse sand (E3548, S1139); S.E. of Cape Vidal, 145 m, medium sand (E7510); do, 165 m, moderately fine sand (E7600); off Mission Rocks, 198 m, medium sand (E4746, S1138).

Extralimital locality data: RÉUNION ISLAND (all MNHN, dredged R. V. *Marion Dufresne*, cruise 32): St DC54, 21°06′S:55°13′E, 80–83 m; St DC56, 21°05′S:55°12′E, 170–225 m; St DC58, 21°03′S:55°10′E, 450 m; St DC86, 20°59′S:55°15′E, 75–90 m; St DC128, 20°51′S:55°36′E, 280–340 m; St DC176, 21°02′S:55°11′E, 165–195 m; St DS178, 21°04′S:55°10′E, 412–460 m.

Ethminolia sculpta (Sowerby, 1897) **comb. n.**

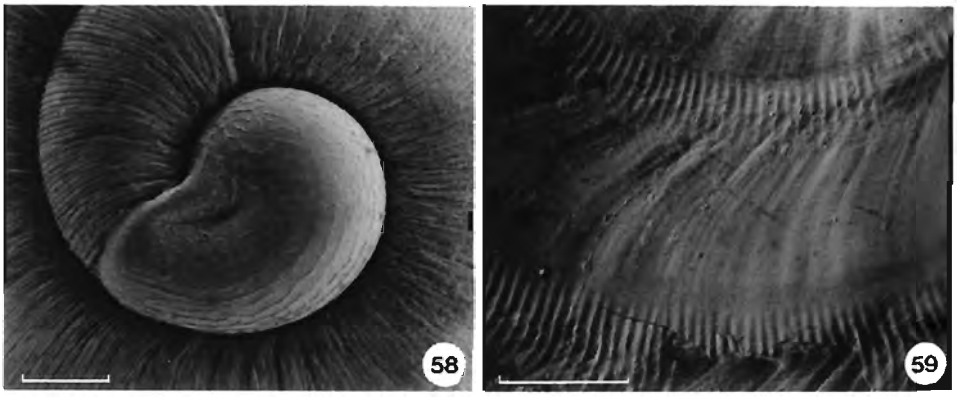
Figs 55–59; Map 7.

Solariella sculpta Sowerby, 1897: 29. Type loc.: the Bluff, Durban Bay.
Minolia sculpta; Kilburn, 1972: 396, figs 3, 4 (lectotype designated).



Figs 55–57. *Ethminolia sculpta* (Sowerby, 1897). Lectotype of *Solariella sculpta* Sowerby, 1897, diameter 4,15 mm (NMSA 1233/T523).

Notes: Kilburn (1972) has adequately redescribed and figured the gross shell morphology of this species. However it cannot be referred to *Minolia* A. Adams, 1860, as that genus has been shown to have a solarielline radula (see Herbert 1987). The radula of the present species, though not examined under SEM, has a very reduced central tooth field and is clearly umboniine (30–35 transverse rows).



Figs 58–59. *Ethminolia sculpta* (Sowerby, 1897). 58, protoconch, bar = 50 μm (NMSA 8947); 59, operculum, bar = 100 μm (NMSA 8947).

The small, beaked protoconch (diameter 180–200 μm) (Fig. 58) with reticulate sculpture is likewise umboniine rather than solarielline. The operculum (Fig. 59) has a radially striate peripheral fringe, but lacks spiral microlirae.

Conchological features in general suggest an affinity with *Ethminolia* and the species seems best referred here. It is not unlike *E. nektonica* (Okutani, 1961) from Japan, but *sculpta* is smaller and has a coarser axial sculpture, a more strongly lirate base and usually has a dark purplish apex. *E. nedyma* (Melvill, 1897), from the Persian Gulf is similar, particularly in apertural view, but lacks strong axial sculpture (Yaron 1976). *E. impressa* (G. & H. Nevill, 1869) [= *Minolia eucoronata* Sowerby, 1905, see Appendix] from Ceylon, has a more weakly sculptured base and has at most fine spiral lirae between the shoulder and the periphery. Kilburn (1972) compared *E. sculpta* with *Minolia plicatula* Murdoch & Suter, 1906, the type species of *Zeminolia* Finlay, 1926, but that species has a much larger protoconch (*ca* 500 μm in diameter) and has since been shown to have a solarielline radula (Herbert 1987).

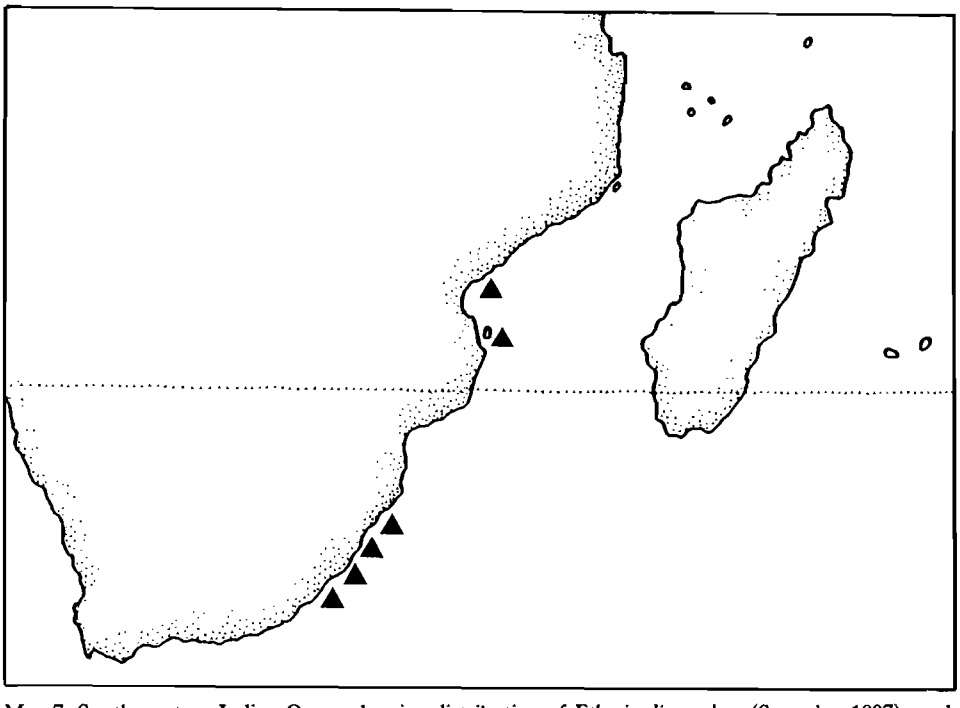
The only live-taken material available was collected many years ago and has been kept dry ever since. Even after rehydration of the bodies using trisodium phosphate, little meaningful anatomical detail can be seen.

Distribution: Although previously obtained only from Durban Bay, the known range has been considerably extended, *viz*: southern Mozambique to south-western Transkei, reaching a depth of nearly 150 m (living specimens to 32 m).

Type material: Lectotype in Natal Museum (NMSA 1233/T523) and two paralectotypes in BMNH (1899.4.14.3562 and 1902.7.30.38).

Additional locality data (all NMSA, unless indicated otherwise): SOUTHERN MOZAMBIQUE: Beira (SAMC 9702); Inhassaro, E. Roscoe (K315); Inhaca Is., R. Kilburn & E. Roscoe (K1806); Maputo (Delagoa Bay), M. de Lanoy Meiyer (A1014). ZULULAND: Kosi Bay, main reef 1–4 km south of estuary mouth, 20 m, underwater pump, dived D. Herbert & R. Broker (S1255); off Hully Point, 30–40 m, fine muddy sand, dredged NMDP (E2901); do, 40 m, very fine muddy

sand, algae, dredged NMDP (E1460); do, 40 m, fine sand, dredged NMDP (E2918); off Gobey's Point, 44–66 m, sand, shell rubble, dredged NMDP (E2898); north of Leven Point, living, 32 m, dredged A. Connell (D212); Leadsman Shoal, outer portion, 25–28 m, dived D. Herbert & NPBP (E6890); off Leven Point, 50–60 m, mud, dredged NMDP (E5874); off Cape Vidal, 30 m, medium sand, shells, dredged NMDP (E3519); Mapelane, beach drift (B4649, D5844, D5845, E817 and J. Marais coll'n); St Lucia lighthouse, 100 m, mud and pebbles, *ex* CSIR Water Research (A5756); off Durnford Point, 120 m, dredged A. Connell (D4496); off Tugela River, 120–146 m, (SAMC A32836). NATAL: off Sheffield Beach, 25 m, fine sand, dredged NMDP (E9364, E9392); do, 28 m, fine sand, dredged NMDP (E9501); Thompson's Bay Pool, Umhlali district, J. Marais coll'n; off Tongaat Bluff, 30 m, fine muddy silt, dredged NMDP (S205); Durban, H. Burnup, R. Kilburn (3333, 5573); Durban (SAMC 9718); Durban Bay, W. Falcon, H. Burnup, R. Kilburn, J. Marais (8948 living, 8947 living, D5984, S3758); Durban Bay, shallow water dredgings, B. J. Young (A1441, B8700, B2086, D670, E1006); Durban Bluff, H. Burnup (1233/T523 lectotype, 1235 topotype); off Durban Bluff, dredged 18–20 m, fine sand, R. Kilburn & R. Fregona (E977); do, J. Marais coll'n: TRANSKEI: off Port St Johns, 30–50 m, mud, worm tubes, organic debris, dredged NMDP (C1070); off Whale Rock, 20–26 m, sand and gorgonians, dredged NMDP (E184); off Nthlonyane River, 51 m, sandy mud, corals, dredged NMDP (C9601).



Map 7. South-western Indian Ocean showing distribution of *Ethminolia sculpta* (Sowerby, 1897); each black triangle represents one or more records.

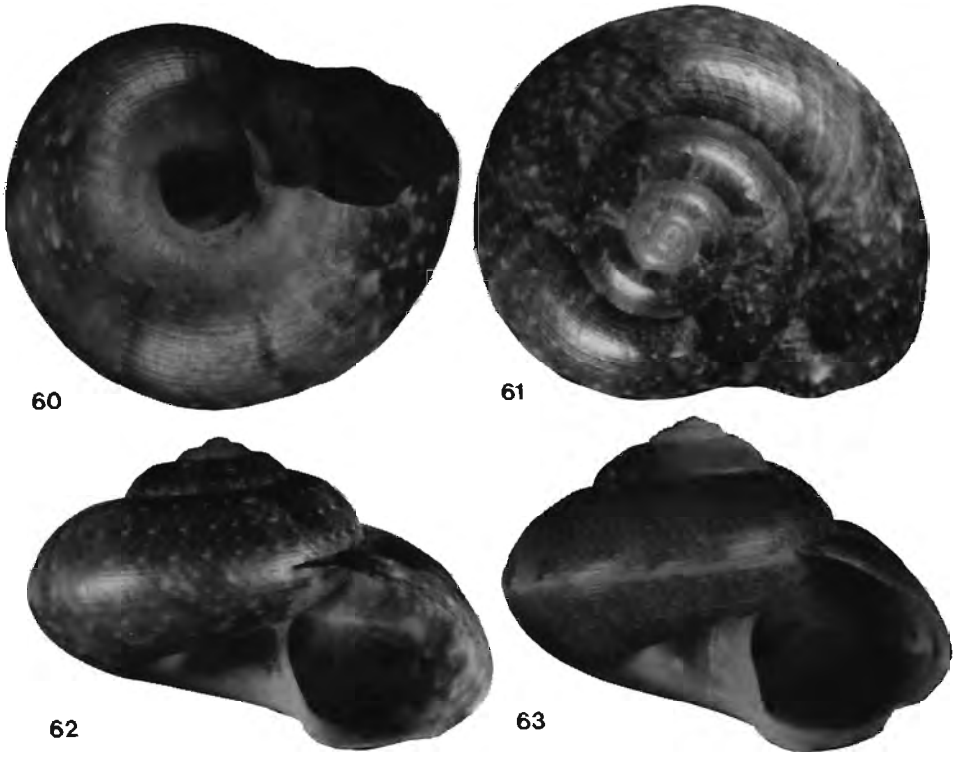
Ethminolia stearnsii (Pilsbry, 1895)

Figs 35, 60–67; Map 8.

Minolia stearnsii Pilsbry 1895: 98. Type loc.: Nemoto, Boshiu, Japan.
Solariella stearnsi [*sic*]; Nomura, 1940: 103.
Sericominolia stearnsii; Kuroda & Habe, 1954: 92, fig. 1 (radula).
Ethminolia stearnsii; Kuroda, Habe & Oyama, 1971: 43, pl. 12, figs 13,14; Springsteen & Leobrera, 1986: 33, pl. 4, fig. 20; Kaicher, 1987: 5052.

Diagnosis: Shell very thin; sculpture very fine, comprising close-set spiral lirae and even more close-set, microscopic axial pliculae; umbilicus with angular margin, but without funicle or callus deposit.

Description: Shell very thin, lustreless, turbiniform to depressed-turbiniform (L/D = 0,70–0,77), teleoconch of up to 5 whorls; whorls rounded, lacking shoulder, but slightly angular at periphery; periphery at mid-whorl; suture at periphery, level; base rounded. Sculpture of numerous very fine, close-set spiral lirae and finer, even more close-set, microscopic axial pliculae; intervals between lirae narrower than lirae themselves, appearing as incised striae; base with somewhat broader, flat-topped lirae. Umbilicus open, of moderate width; margin angular, very slightly thickened, made irregularly pliculate by growth-lines;



Figs 60–63. *Ethminolia stearnsii* (Pilsbry, 1895). 60–62, lectotype of *Minolia stearnsii* Pilsbry, 1895, diameter 9,9 mm (ANSP 70786); 63, specimen from northern Zululand, diameter, 6,6 mm (NMSA D8744).

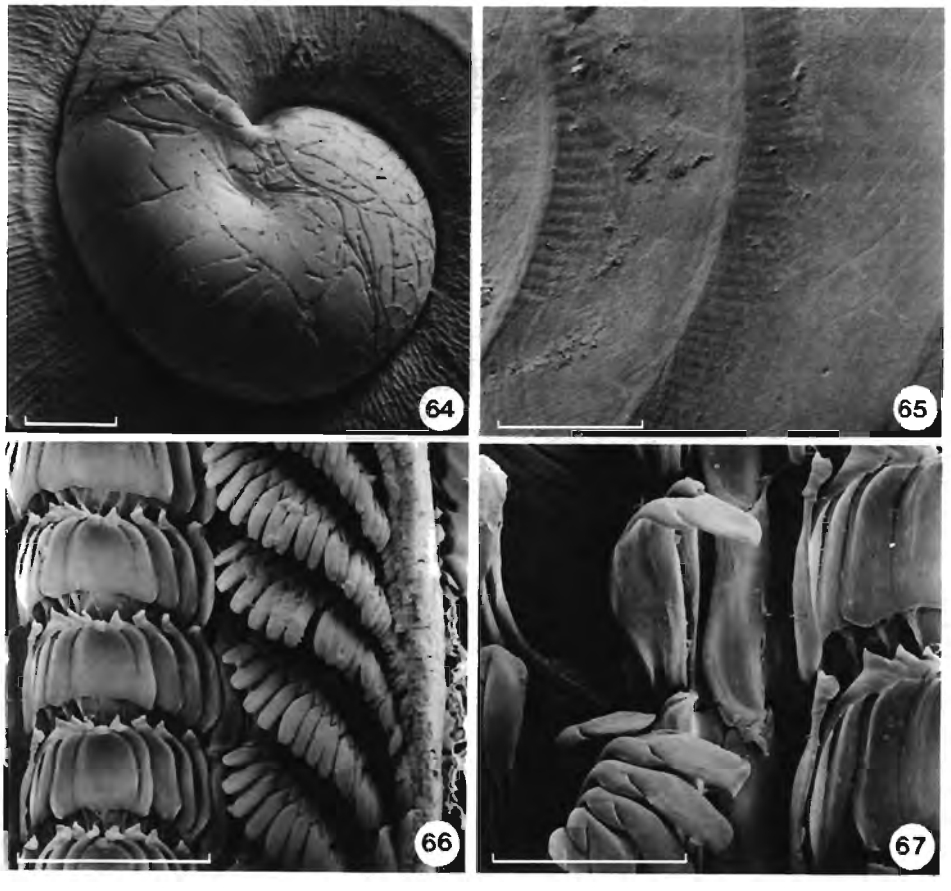
interior variably lirate, lacking funicle or callus deposit. Aperture subquadrate; columella lip straight for most of its length, parietal lip convex; outer lip smooth, prosocline above periphery, orthocline below; interior with very thin layer of nacre.

Protoconch (Fig. 64): Umboniine, but with relatively poorly developed apical beak, reminiscent of *Ethalia*; diameter ca 200 μm.

Colour: Variable, some specimens predominantly orange-red others with whitish ground, fine zig-zag lines and blotches of orange-red or olive-green, lirae usually with numerous white flecks.

Dimensions: Largest NMSA specimen, diameter 7,0 mm, length 5,0 mm, but probably not fully grown.

Operculum (Fig. 65): Corneous; multispiral, but with relatively few whorls; nucleus central; peripheral fringe radially striate; spiral microlirae absent.



Figs 64–67. *Ethminolia stearnsii* (Pilsbry, 1895). 64, protoconch, bar = 50 μm (NMSA E2246); 65, exterior surface of operculum lacking microscopic spiral lirae, bar = 100 μm (NMSA D8046); 66, 67, radula – half row and latero-marginal area (latero-marginal plated arrowed), bars = 100 μm and 50 μm respectively (NMSA S3429); all dredged northern Zululand.

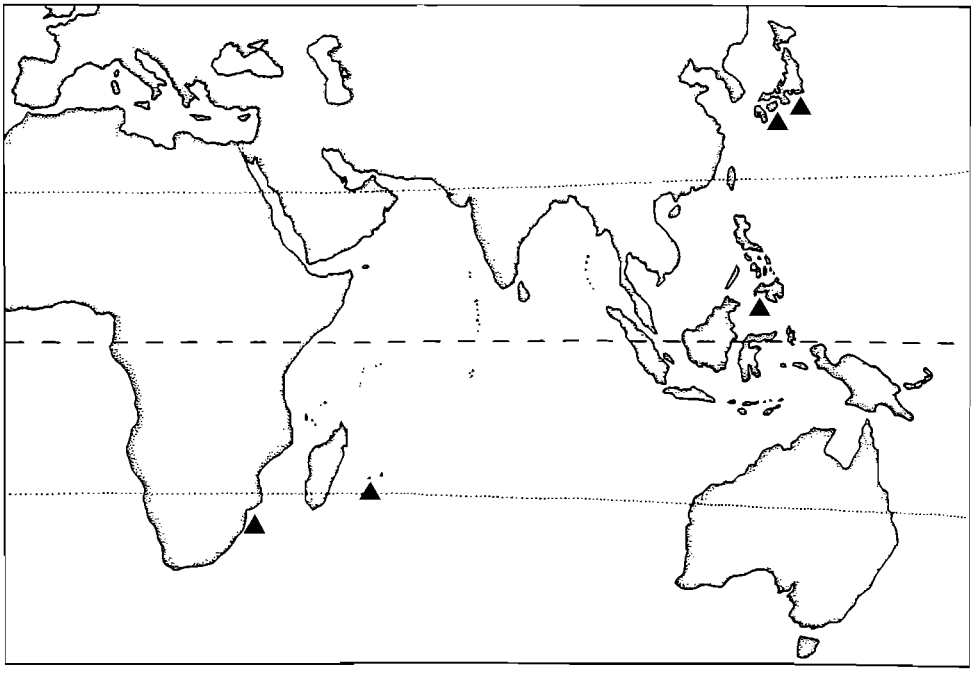
Radula (Figs 66–67): Formula ∞ + (1) + 5 + 1 + 5 + (1) + ∞; ± 40 transverse rows; rachidian and laterals retaining relatively well developed base plates and rudimentary shafts; tooth overlap extensive, but simple. Marginals numerous with apices recurved; cusps spatulate with a well developed thumb-like denticle proximally on the outer edge; first marginal stout with a reduced cusp, forming a latero-marginal plate.

External anatomy (Fig. 35): Body white to pale yellowish-white. Head with distinct forehead separating cephalic tentacles; tentacles micropapillate; no cephalic lappets or intertentacular fold; snout relatively well developed, not obviously tapered and with coarse, subterminal papillae; lips thick, roundly lobed; eye stalks of moderate length, not fused to cephalic tentacles, eye large, black, terminal; no right post-optic tentacle. Left neck lobe a thin flap of tissue the free margin of which bears ± 15 fine, micropapillate digitations, lobe broader and digitations larger anteriorly, lobe not fused to eye stalk; right neck lobe a broad tissue flap, rolled to form an exhalant siphon, not fused to base of right eye stalk. Epipodial tentacles finely papillate, 4 on each side, arising from underside of epipodial fold, one just behind neck lobe, another near start of operculum and two beneath operculum; epipodial fold a thin smooth-edged flap which joins posteriorly in the mid-line; epipodial sense organs present, one some distance beneath anterior edge of each neck lobe, another between first and second epipodial tentacles and one at the base of the each of the three posterior tentacles. Foot truncated anteriorly, tapering to a point posteriorly; propodium bifid, lateral portions drawn out into triangular lobes; sole constricted posterior to propodial lobes, but broadening to its maximum width just behind this; sides of foot smooth.

Ctenidium: long, bipectinate for most of its length, afferent ctenidial membrane extending well beyond junction of transverse pallial vein and afferent ctenidial vessel leaving only the distal ¼ of the ctenidium free. Filaments on left of ctenidial axis reduced, those on right of axis slender with expanded tips.

Distribution: Zululand, Réunion and Japan; intertidal to 225 m (living specimens 10–65 m).

Regional locality data (all NMSA): ZULULAND: Kosi Bay, main reef 1–4 km south of estuary mouth, 20 m, underwater pump, dived D. Herbert & R. Broker (S1254); do, 20–24m, underwater pump, dived D. Herbert & K. Bloem (S1257, S2907); off Kosi Bay, living, 65 m, sponge, gorgonians, medium sand, dredged NMDP (D8046); off Boteler Point, living, 58–61 m, sand and pebbles, dredged NMDP (S3431, S4183); do, 70 m, coral rubble, dredged NMDP (E2246); N.E. of Dog Point, 56–57 m, sand, *Lithothamnion* pebbles, dredged NMDP (S5048); do, living, 65 m, sand and *Lithothamnion* pebbles, dredged NMDP (S3429); off Jesser Point, 42 m, medium sand, dredged NMDP (D8744); Sodwana Bay, Two-Mile Reef, living, sorted from stone washings, 10–15 m, dived D. Herbert & R. Broker (E771); off Liefeldt's Rocks, 50 m, medium sand with some stones, dredged NMDP (E3414); do, 50 m, dead coral rubble, *Lithothamnion*, medium sand, dredged NMDP (E4260); north of Leven Point, 32 m, dredged A. Connell (D4933); off Leven Point, 50–60 m, mud, dredged NMDP (E5872).



Map 8. Indian Ocean and western Pacific Ocean showing distribution of *Ethminolia stearnsii* (Pilsbry, 1895); each black triangle represents one or more records.

Extralimital locality data: RÉUNION ISLAND: 21°05'S:55°12'E, 170–225 m, dredged R. V. *Marion-Dufresne*, cruise 32, 1982, st. DC56 (MNHN).

Type material: Three syntypes are present in the ANSP (No. 70786). One is here figured and designated lectotype (Figs 60–62).

Remarks: The above description is based only on southern African material and this I somewhat hesitantly refer to *E. stearnsii*. The type specimens of the species, though sculptured by fine growth-lines, seem to lack the regular microscopic axial pliculae of local shells and are larger. All three types, however, are rather worn and none of the southern African specimens can be considered adult. I can find no obvious characters by which to separate this local material from *E. stearnsii* and therefore refer it to that species. Specimens dredged off Réunion Island by the MNHN, though from considerably deeper water, may also be referred to this species.

As stated in the introductory remarks regarding this genus, *E. stearnsii* appears to be one of a cluster of poorly known species which possess larger, more elevated and thinner shells than is typical of *Ethminolia*. Other members of this group include *Ethminolia eilikrines* (Melvill, 1891), from the Philippines, and *E. vitiliginea* (Menke, 1843) from southern Australia. The former is more elevated, noticeably shouldered and has a coarser spiral sculpture than *stearnsii* (Fig. 133). *E. vitiliginea* is perhaps the most similar species, but has a less close-set spiral

sculpture and, like *eilikrines*, has shouldered whorls (Fig. 132). *'Monilea' vernicosa* Gould, 1861 (holotype, USNM 24177), from southern Japan and the Philippines, is also similar, but is easily distinguished by its umbilical funicle (Fig. 136).

Tribe Umboniini H. & A. Adams, 1854

Diagnosis: Umboniines with a monopectinate ctenidium and frequently a number of other derived character states such as an elaborately branched or hypertrophied left neck lobe, a reduced forehead, small tapering snout, elongate eye stalks (most genera) and very reduced teeth in the central field of the radula.

Remarks: This tribe, as here constituted, comprises an assemblage of more highly derived umboniine genera united by their possession of a monopectinate ctenidium. It is clearly possible to further subdivide this group, separating out bankiviine, lirulariine and umboniine (*s.s.*) genera (cf. Hickman & McLean 1990). However, there are a number of additional genera including *Inkaba* gen. n., *Pseudominolia* gen. n., *Zethalia* and *Antisolarium* which do not fit in to any of these existing subgroupings, and sill others which may well have monopectinate ctenidia, but about which no anatomical data are available, eg. *Vanitrochus, Isanda* and *Ethaliella*. I consider it unwise to propose a new suprageneric taxon (or perhaps two taxa) for the two local genera *Inkaba* and *Pseudominolia* when the global picture is still inadequately known and for the purposes of this revision I have therefore chosen not to split this group further. The reasons for including *Lirularia* in the Umboniinae have been given previously (page 388).

Inkaba gen. n.

Type species: *Inkaba tonga* sp. n.

Diagnosis: Shell small, trochiform, lacking an umbilical funicle and/or heavy callus deposit; radula relatively short (35–40 transverse rows), cusps of marginal teeth multidenticulate; cephalic tentacles separated by a distinct forehead; digits of left neck lobe unbranched; ctenidium monopectinate; operculum lacking spiral microlirae.

Remarks: In terms of shell morphology this monotypic genus most closely resembles the smaller species of *Ethminolia*, although it is somewhat more elevated. However, its monopectinate ctenidium allies it more closely with *Pseudominolia* and other more highly derived umboniine taxa. It differs from these in possessing a distinct forehead between the cephalic tentacles and in retaining unbranched digits on the left neck lobe. It is perhaps most similar to *Lirularia* Dall, 1909, but members of that genus possess only three pairs of epipodial tentacles, have elongate cusps on the marginal teeth, and thicker, more globose shells with a narrower umbilicus. *Inkaba* seems to represent a level of anatomical organisation intermediate between that of the Monileini and that of *Pseudominolia*.

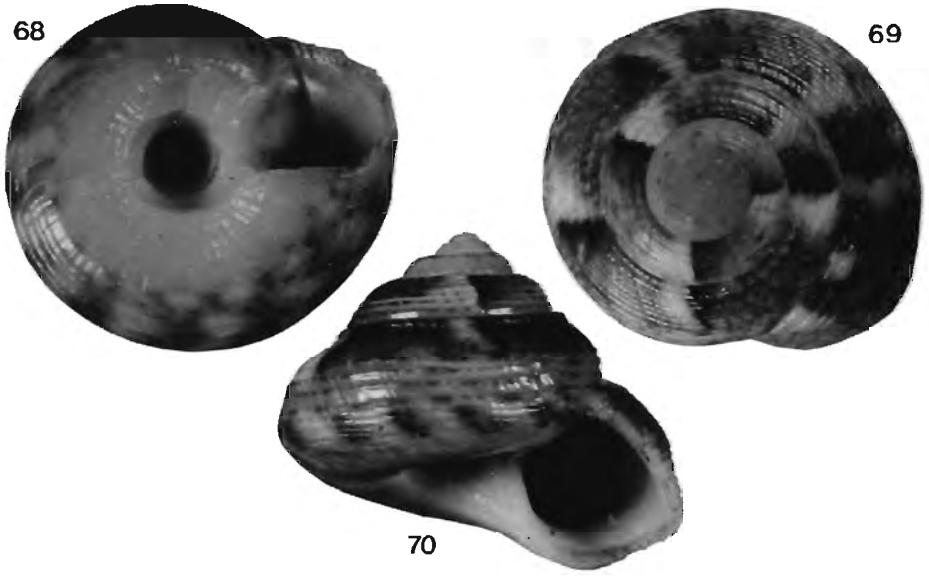
Etymology: *Inkaba* Zulu, an umbilicus (feminine).

Inkaba tonga sp. n.

Figs 68–76; Map 9.

Diagnosis: Shell small, trochiform, relatively elevated; periphery well below mid-whorl, base flattened; sculpture of spiral lirae, uppermost lira forming a beaded subsutural cord; base for the most part smooth; umbilical margin angular and pliculate.

Description: Shell small, trochiform, relatively solid, height moderate (L/D = 0,75–0,83); teleoconch of up to 5,5 whorls, periphery roundly angled, well below mid-whorl; base somewhat flattened; suture at periphery, level. Sculpture primarily spiral; early whorls with weak spiral lirae; lirae strengthen and become more numerous with growth; uppermost lira on fourth whorl developing into a subsutural cord; cord variable in strength, but often giving later whorls a stepped profile just below suture; subsutural cord often finely beaded; body whorl with 10–15 close-set spiral lirae between subsutural cord and periphery, those near periphery somewhat stronger and more widely spaced, intervals sometimes with weaker intermediaries; base with *ca* 3 lirae near periphery, remainder with at most obsolete lirae. Axial sculpture of indistinct subsutural pliculae which cause beading of subsutural cord, and fine, but irregularly spaced collabral growth-lines; growth scars also common; base with pliculae radiating from umbilicus, pliculae particularly strong in juveniles; microscopic scratch-like axial sculpture also present. Umbilicus open; margin angular, set off by spiral cord, sometimes also with 1–2 spiral lirae around this; cord variably granulated by pliculae; interior with a variable number of fine spiral lirae. Aperture quadrate; outer lip nearly smooth; basal lip notched at umbilical margin; columella without callus deposit.



Figs 68–70. *Inkaba tonga* sp. n., holotype, diameter 5,0 mm (NMSA E1687/T39).

Protoconch (Fig. 72): typically umboniine and with some superficial reticulation evident; diameter 150–200 μm.

Colour: Variable, but typically with white to greyish-white ground colour suffused with patches and spots of pale orange-brown; paired axial flames of white and moderate to dark olive-brown radiate from suture; periphery with a belt of alternating red and white spots; base greyish-white with spots, blotches and bands in white, red, orange or brown, usually less densely patterned than apical surface; umbilicus without colour pattern. Some specimens coloured entirely in shades of grey on a near white ground.

Dimensions: Holotype, diameter 5,0 mm, length 4,0 mm; largest specimen, diameter 5,1 mm, length 3,9 mm.

Operculum (Figs 71, 73): pale corneous, almost colourless, transparent; whorls broad, marked by oblique growth-lines; each whorl with a well developed, radially striate peripheral fringe, fringe often iridescent; spiral microlirae lacking.

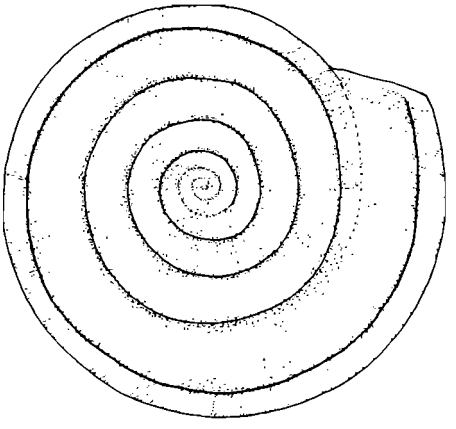
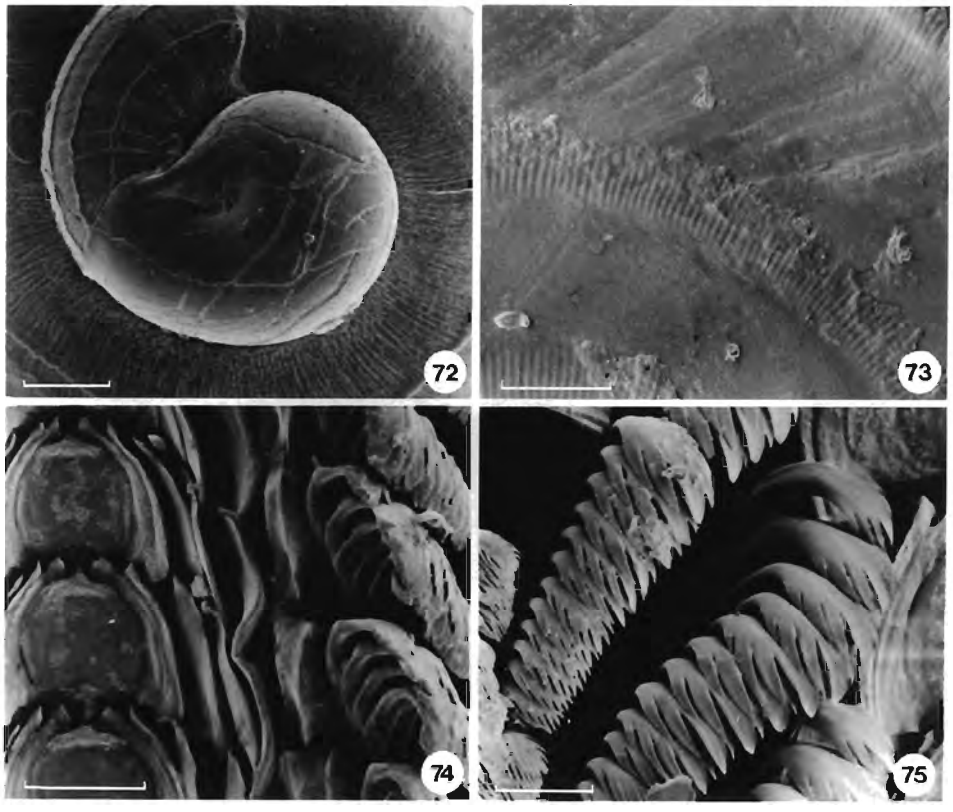


Fig. 71. *Inkaba tonga* sp. n., operculum, diameter *ca* 1,6 mm.

Radula (Figs 74–75): Formula ∞ + (1) + 5 + 1 + 5 + (1) + ∞, 35–40 transverse rows; basal plates of rachidian and laterals remaining well defined, but lacking shafts and cusps; tooth overlap simple but extensive; rachidian subcircular to roundly quadrate; laterals triangular to rhomboidal, sharply pointed where shafts would arise (less obvious in light microscope preparations); marginals numerous, distally expanded, flattened and curled over, apex coarsely denticulate on its outer edge, finely so on inner edge; a latero-marginal plate is present between the outer lateral and the marginals, this has a very reduced shaft with no cusp and appears to be a modified first marginal.

External anatomy (Fig. 76): Body pale yellowish-white, cephalic tentacles, eye stalks, neck lobes, sides of foot and mantle edge with blotches of white pigment; dorsal surface of propodium with some black pigmentation. Head with distinct forehead separating cephalic tentacles, tentacles papillate, papillae on distal half of tentacle apparently arranged in rings; snout moderately well developed, but



Figs 72–75. *Inkaba tonga* sp. n. 72, protoconch, bar = 50 μm (NMSA D7407); 73, operculum, bar = 100 μm (NMSA E1369); 74, radula, half row, bar = 20 μm (NMSA E1369); 75, radula, cusps of inner marginal teeth, bar = 10 μm (NMSA E1369).

subterminal papillae few in number and restricted to lateral margins of snout; lips relatively thin, split mid-ventrally; cephalic lappets absent; eye stalks long, distally swollen to accommodate the well developed eye, not fused to cephalic tentacles; no right post-optic tentacle. Left neck lobe a series of *ca* six unbranched, nonpapillate tentacles; posterior tentacles smaller than anterior ones; right neck lobe not fused to eye stalk, very broad anteriorly and rolled to form a relatively long exhalant siphon; siphon capable of being extended beyond snout. Epipodial tentacles micropapillate, 4 on each side, arising from underside of epipodial fold, one just behind neck lobe, another near start of operculum and two beneath operculum; epipodial fold a thin, smooth-edged flap which joins posteriorly in the mid-line; epipodial sense organs present and relatively large, one beneath each neck lobe, another between first and second epipodial tentacles and one at the base of the each of the three posterior tentacles. Foot truncated anteriorly, tapering to a point posteriorly; propodium bifid, lateral portions drawn out into lobes; sole constricted posterior to propodial lobes, but broadening to its maximum width just behind this; sides of foot smooth.

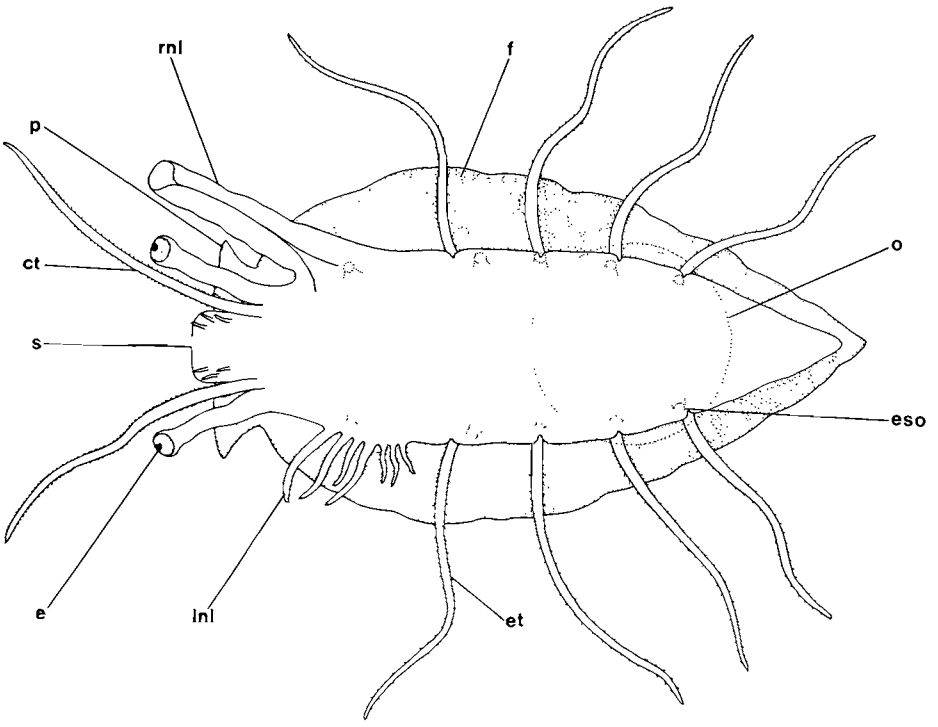


Fig. 76. *Inkaba tonga* sp. n. Diagrammatic representation of external anatomy: ct, cephalic tentacle; e, eye; eso, epipodial sense organ; et, epipodial tentacle; f, foot; lnl, left neck lobe; o, operculum; p, propodium; rnl, right neck lobe; s, snout.

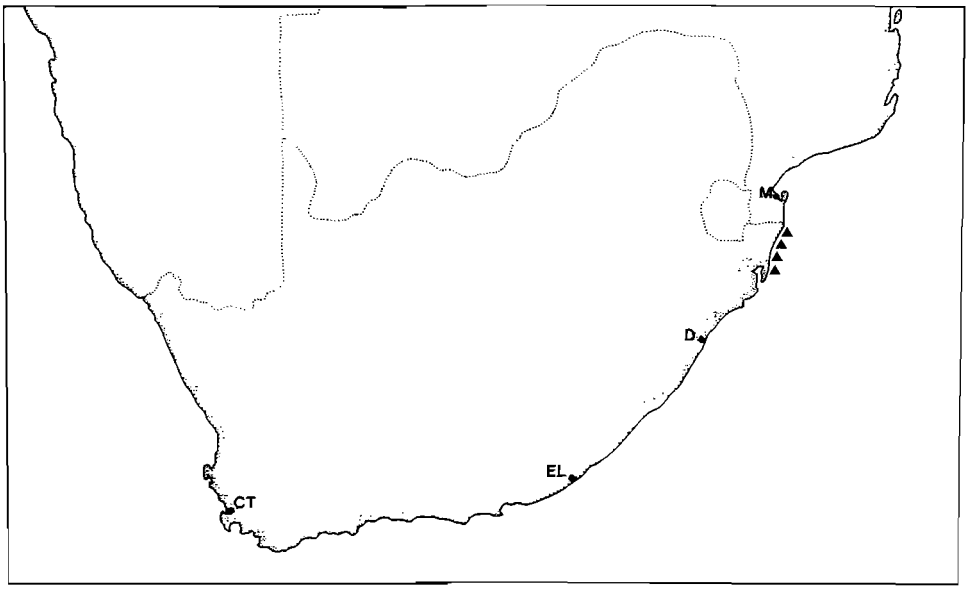
Ctenidium: Monopectinate; attached to wall of mantle cavity throughout its length; filaments elongate, but not greatly so.

Distribution: Known only from Zululand; Kosi River mouth south to Leven Point, 40–100 m (living specimens the same), varied substrata.

Type material (all dredged NMDP, dead unless indicated otherwise): Holotype, NMSA E1687/T39, S.E of Kosi River mouth, northern Zululand (26°56,9′S: 32°54,6′E), 50 m, fine sand, shells; paratypes 1–2, NMSA E1688/T40, same data as holotype; paratypes 3–13, NMSA E1689/T41, S.E. of Kosi River mouth, Zululand 45–50 m, fine sand, algae, gorgonians; paratypes 14–18, NMSA E1690/T42, do, living, 45–47 m, red algae, sponges; paratypes 19–26, NMSA E1691/T43, off Gobey's Point, Zululand, living, 55-100 m, sand, shell rubble; paratypes 27–30, NMSA E1692/T44, off Kosi River mouth, Zululand, 47 m, dead coral, sponges, large algae; paratypes 30–40, growth series, NMSA E1693/T45, S.E.of Kosi River mouth, 50 m, algae, shells; paratypes 41–54, NMSA E1694/T46, do, living, 50 m, fine sand; paratypes 55–75, NMSA E1695/T47, off Kosi River mouth, living, 50 m, coarse sand and shells.

Additional locality data (all NMSA, dredged NMDP, dead unless indicated otherwise): ZULULAND: off Kosi River mouth, 45 m, fine muddy sand

(D6027); do, living, 47 m, dead coral, sponges, large algae (E1396); do, 50 m, medium sand, algae (D6864); do, living, 75 m, coral rubble, sandstone, marine growths (E1408); off Kosi Bay, 50 m, shell grit, dredged CSIR Water Research (A5947, A5955); S.E. of Kosi River mouth, 50 m, fine, slightly muddy sand (D8280); do, living, 50 m, fine sand, shell rubble, *Codium* (D7317, E1464); do, 50 m, fine slightly muddy sand (D7790); do, living, 45–47 m, red algae, sponges (E1389); do, 50 m, fine sand, shells (D8425); do, 50 m, coarse sand, shells (D6939); do, 50 m, algae, shells (D6078, E1377); do, 50 m, fine sand (D7043); do, 45–50 m, fine sand, algae, gorgonians (D8893, E1369); do, 50 m, fine sand (D8626); do, living, 40 m, fine sand (D8236); do, 40 m, fine sand (E1757); off Boteler Point, 66 m, sand, rocks (S3846); do, 70 m, some coarse sand, some shell rubble (D7407); do, 70 m, coral rubble (E1702); off Dog Point, 70 m, sandstone conglomerate (E1746); off Lala Neck, living, 75 m, coarse sand, sandstone (S3489); off Island Rock, 62 m, sandstone, coral, marine growths (E2922); off Hully Point, 50 m, fine sand (D7566); do, living, 60 m, shell rubble (E1728); do, 40 m, fine sand (D9050); off Gobey's Point, living, 55–100 m, sand, shell rubble (E1438); do, living, 44–66 m, sand, shell rubble (E2899); off Jesser Point, living, 68 m, sponge, coral rubble (E1351); do, 48–58 m, sand, shell rubble (D6535); do, 52–58 m, medium sand (D8518); off Sodwana Bay, 49–53 m, sand (S4731); do, living, 70 m, coral rubble (S3919); do, dredged CSIR Water Research, (A5096, D2217); N.E. of Gipsy Hill, living, 63–70 m, sandstone rocks and marine growths (S3472); do, 65–70 m, broken shell (E7469); off Gipsy Hill, 47–50 m, fine sand (S1135); do, living, 52 m, fine sand (E6950); do, living, 63–70 m, sandstone



Map 9. Southern Africa showing distribution of *Inkaba tonga* sp. n.; each black triangle represents one or more records.

rocks, sand and marine growths (S3472); off Leven Point, 50–60 m, mud (E4132, E5871).

Remarks: *I. tonga* is easily recognised amongst local species by its more conical shape, pliculate umbilicus and beaded subsutural cord. *Ethminolia eudeli* (Deshayes, 1863) from Réunion Island is similar, but is larger (up to 6,5 mm in diameter – MNHN material) and less elevated, and has finer, more close-set spiral sculpture which is also present on the base, and lacks a distinct, beaded subsutural cord. A syntype is here figured (Figs 117–119). *E. impressa* (G. & H. Nevill, 1869) [= *Minolia eucoronata* Sowerby, 1905 see Appendix], from Ceylon, is more depressed, has a distinct peripheral keel and has much coarser beading on the subsutural cord and umbilical margin.

Etymology: Named after the amaThonga people who inhabit the east coast of southern Africa, from St Lucia in Natal north to the Save River in Mozambique.

Pseudominolia gen. n.

Type species: *Solariella splendens* Sowerby, 1897.

Diagnosis: Shell trochoid-turbiniform; whorls frequently shouldered, sculptured primarily with spiral cords or lirae; umbilicus open, lacking a funicle and/or heavy callus deposit; protoconch with well developed apical beak; radula very thin and delicate, marginal teeth broad distally with multidenticulate cusps; left neck lobe a series of branching tentacles; ctenidium monopectinate; external surface of operculum with numerous close-set spiral microlirae.

Radula: The radula is described in detail for *P. splendens*. It has the typical reduced central field characteristic of the subfamily and is very thin and delicate. It is shorter than that of most monileine genera (40–50 transverse rows) and the base plates of the rachidian and laterals are less well defined. The most striking difference between the radula of *Pseudominolia* and that of monileine taxa is in the form of the marginals which have broader less elongate cusps (breadth greater than half of length) with several well defined denticles on both margins.

External anatomy (Figs 77, 101–103): Described in detail for *P. splendens*. *Pseudominolia* exhibits the typical shared derived features that characterise the Umboniinae, such as the subterminal snout papillae, elongated eye stalks and bifid propodium, but shows additional anatomical apomorphies, such as the narrow forehead, branched left neck lobe tentacles and monopectinate ctenidium, which distinguish it from the less specialised monileine genera and ally it more closely with *Umbonium*, *Zethalia* and *Antisolarium*. *Umbonium* and *Zethalia*, however, show additional anatomical and conchological features which set them apart from *Pseudominolia*, for example the hypertrophied left neck lobe and callus filled umbilicus. Anatomically *Pseudominolia* is clearly at a stage intermediate between more 'primitive' genera such as *Ethalia* and the highly derived *Umbonium*.

Operculum (Figs 78–79): Described in detail for *P. splendens*. Similar to that of other umboniine genera, but with fine, close-set spiral lirae on the external surface (Figs 88, 95).

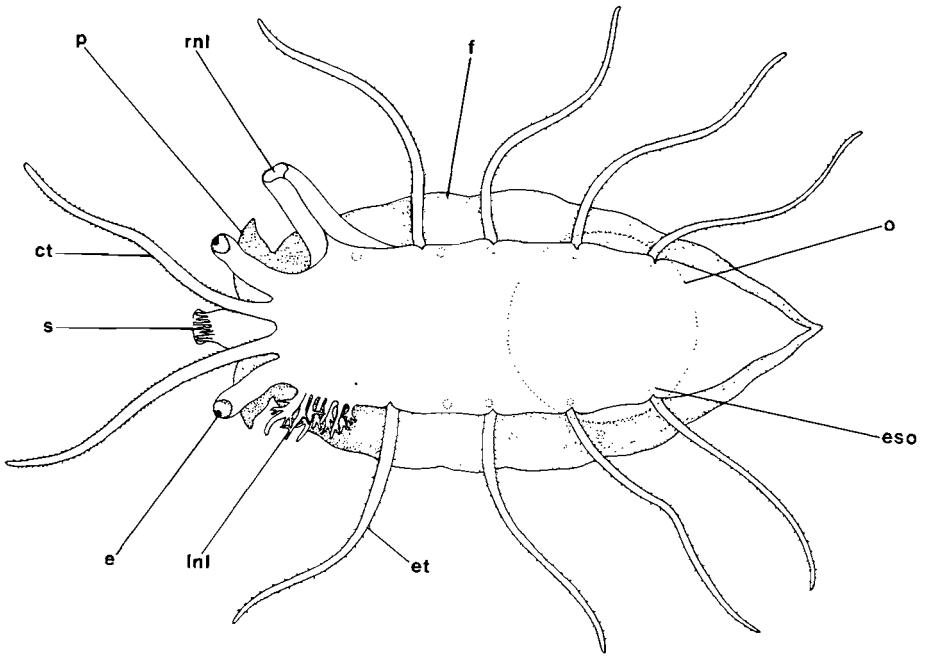
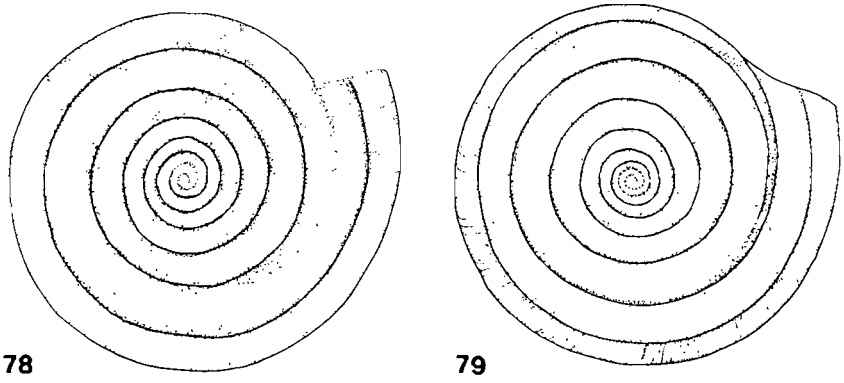


Fig. 77. *Pseudominolia splendens* (Sowerby, 1897). Diagrammatic representation of external anatomy: ct, cephalic tentacle; e, eye; eso, epipodial sense organ; et, epipodial tentacle; f, foot; lnl, left neck lobe; o, operculum; p, propodium; rnl, right neck lobe; s, snout.

Remarks: In terms of its conchological form, monopectinate ctenidium, reduced forehead and snout, and non-hypertrophied left neck lobe, *Pseudominolia* shows considerable similarity with *Antisolarium* and the two are almost certainly closely related. *Antisolarium*, however, has a left neck lobe with unbranched digits and has a radula with modified marginal teeth which possess a well developed, triangular expansion of the shaft below the recurved cusp creating a semitubular



Figs 78–79. *Pseudominolia* operculum; 78, *P. articulata* (Gould, 1861), diameter *ca* 2,0 mm; 79, *P. splendens* (Sowerby, 1897), diameter *ca* 4,0 mm.

Pondoland, R. Kilburn (9038); Mzamba, beach-drift, R. Kilburn & D. Herbert, J. Marais (D2969, S3759); Mbotyi, beach-drift, R. Kilburn & D. Herbert (C8395) and J. Marais coll'n; off Mbotyi, living, 42–45 m, worm tubes, some sponges (C331); do, living, 45–50 m, mixed mud, sand, some rocks, gorgonians, few sponges (C7947); do, living, 50 m, mixed sand, mud, abundant worm tubes (C1751, C1796, C303); do, 50 m, sand (C9599); off N'tafufu River, living, 50 m, mud, sand (C9598); off Port St Johns, living, 38–40 m, mud, worm tubes, organic debris (C1114); do, 30–50 m, mud, worm tubes, organic debris (C1080); do, living, 40–50 m, worm tubes and organic debris, less mud (S3711); off Mgazi River, 25 m, firm sand (C7972); do, 48 m, mud (C7970); off Ubombo, living, 40–45 m, coarse sand, soft corals, brachiopods (C7942); off Whale Rock, living, 20–26 m, sand and gorgonians (C7905); do, 58–60 m, mixed sand and mud (C7930); do, living, 70–73 m, marine growth, calcareous debris (C9600); do, living, 90 m, sponge rubble, small pebbles (C9597); Coffee Bay, beach-drift, R. Kilburn (A2984); off Mncwasa Point, living, 25–23 m, fine sand, gorgonians (C7918); off Nthlonyane River, living, 51 m, sandy mud, corals (C7902, C2882); off Mbashe River, 50–52 m, shell fragments (E1699); off Nqabara Point, 48–50 m, black mud (C5030); do, living, 90 m, sponge and sand (C4131); off Shixini Point, 45–48 m, muddy sand (C4389); off Qora River, 45 m, coarse sand, numerous hermit crabs (C4004); off Sandy Point, 66 m, grey mud (C4568); do, 48–50 m, fine sand (C4587); do, living, 450–498 m, fine sand and stones (C7887)(suspect data); off Qolora River, living, 50 m, fine sand and mud (C4689). EASTERN CAPE: off Gonubie, 40 m, marine growths, rocks (B8303); off Bonza Bay, living, 60 m, muddy sand, (B7887); do, 60 m, sandy mud (B8035); off East London, 30–35 m, marine growths (B7941); do, living, 40 m, worm cases and hermit crabs (S3712); do, living, 50 m, grey muddy sand, worm tubes, brittle-stars (B7891); do, 60 m, grey mud, worm tubes (B8492); do, 70 m, sand with mud lumps (B7915); do, 70 m, grey sandy mud, astrorhizid foraminiferans (B8349); do, 70 m, muddy sand with lumps of black mud (B8278); Port Alfred, J. Hutt coll'n (D2330); Port Elizabeth, harbour dredgings, F. Greave (A5574); Algoa Bay, New Brighton Beach, raised beach deposit, 9 m level (last interglacial) (D4363); Jeffrey's Bay, R. Kilburn (9035). SOUTHERN CAPE: Struis Bay, Cape Agulhas, beach drift, E. Roscoe (E6454); off Struis Bay, living, 32 m, sponges and some stone (S3579); FALSE BAY: 'False Bay' dredgings, C. Connolly (A231); do, living, 24 m, sand, dredged, Th. Mortensen (ZMUC); central False Bay, 40 m, fine sand and worm tubes (S3561); do, living, 41 m, fine sand and worm tubes (S3581); do, living, 54 m, sand (S3553); Gordon's Bay, beach-drift, R. Kilburn, C. Connolly (A2989, B6885); off Macassar Beach, dredged 18 m, C. Connolly (A3108, A3109); S.E. of Seal Is., 42 m, fine sand, shell (S3522); Muizenberg, living, C. Connolly (6644); off Fish Hoek, dredged 18–22 m, R. Kilburn & J. Dichmont (8638); do, living, 18–22 m (D1972); Fish Hoek, C. Connolly (A3379); north of Simonstown, living, 28 m, sand and shell (S3543); between Seal Is. and Simonstown, living, 40 m, fine sand and worm tubes (S3744); off Simonstown, 31 m, sand, shell (S3626); Glencairn, intertidal swimming pool, C. Connolly (A4177); Buffels Bay, 5 m, living, dived V. Millard (E828, S3374).

Type material: The holotype of *Margarita articulata* Gould, 1861, is in the USNM (C121). It is here refigured (Figs 80–82). Types of *Solariella algoensis* Thiele, 1925 and *Minolia bleeki* Thiele, 1925, are presumably in the ZMHB.

Remarks: A very variable species in terms of shell height, colour and sculpture. The most striking differences occur in the number and strength of the spiral cords. Specimens from Natal and Transkei tend to be smaller and have fewer (two in beach-drift and shallow water specimens, three in deeper water forms), stronger spiral cords above the periphery than typical specimens from False Bay. Axial sculpture is generally weak, but three lots, two from False Bay and one from Port Elizabeth, contain specimens with well developed axial pliculae over most of the shell surface. Colour is likewise variable, beached specimens from Transkei having the most vivid coloration, False Bay material is generally not so boldly marked. It is possible that more than one species is involved here, certainly specimens from either end of the range are easily distinguishable (compare Figs 82 and 84), but I have been unable to find characters which show consistent, non-intergrading differences by which the material can be subdivided.

Barnard (1963) has commented on the synonymy of this species and I agree with his views. After examination of the type material I can confirm that *Margarita dilecta* A. Adams, 1855, is clearly a distinct species (see Appendix) and no southern African material resembling it has been found during the course of this study. *P. articulata* differs in having a more well developed shoulder, a less strongly angled umbilical margin and in lacking obvious beading on the two uppermost spiral cords.

The status of *Minolia bleeki* Thiele, 1925, requires further study. Although quite possibly a synonym, I have been unable to examine the type material at the ZMHB in order to confirm this. Thiele's *Solariella algoensis* is simply the axially pliculate form. *P. articulata* is a widely distributed species in southern Africa distinguished by its well developed spiral sculpture and relatively elevated shape. The most similar local species is *P. splendens* (Sowerby, 1897), but that is larger, more glossy and has a smooth base and a crenulate shoulder cord on the early whorls. Elevated specimens resemble *Minolia gradata* Sowerby, 1895, from Karachi, but that species has a more coarsely sculptured base (syntype figured by Yaron 1979). *Minolia holdsworthana* G. & H. Nevill, 1871, from Sri Lanka, is much smaller and has a less rounded base, fewer basal lirae and a much stronger spiral cord bordering the umbilicus (lectotype designated and figured by Herbert 1989).

Pseudominolia splendens (Sowerby, 1897) **comb. n.**

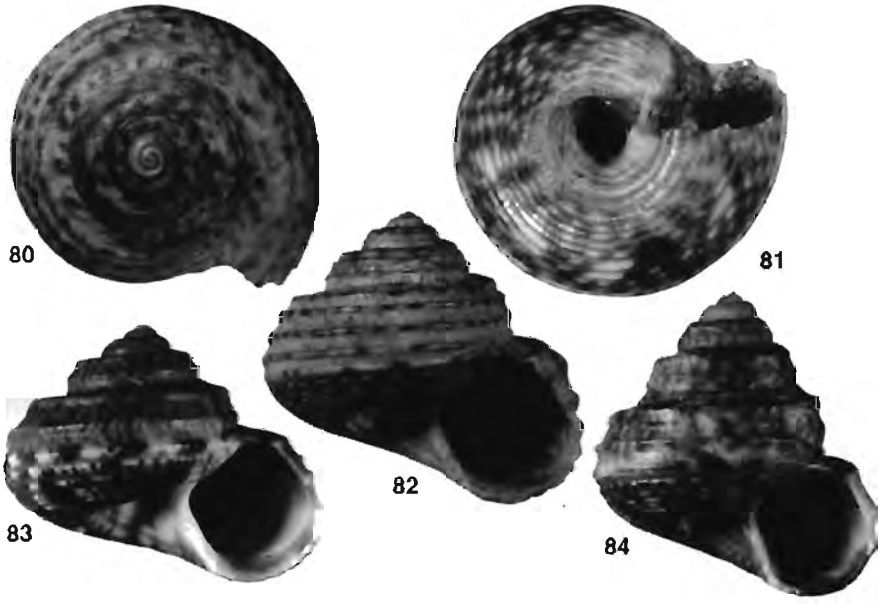
Figs 77, 79, 91–104; Map 11.

Solariella splendens Sowerby, 1897: 18, pl. 6, fig. 21; Dautzenberg, 1923: 56; *idem*, 1929: 334(540). Type loc.: 'Natal (Isipingo)'.

Minolia splendens; Thiele, 1925: 53; Barnard, 1963: 233, fig. 10a (radula); Kensley, 1973: 40, fig. 88; Kilburn & Rippey, 1982: 41, pl. 8, fig. 18.

Minolia variegata Odhner, 1919: 32, pl.2, figs 26–28; Kilburn, 1975: 577, fig. 1; Dautzenberg, 1923: 56; *idem*, 1929: 334(540), **syn. n.** Type loc.: Tamatave, Madagascar, sand, 20–25 m.

Diagnosis: Shell glossy when fresh, adult diameter often >10,0 mm, moderately elevated (L/D = 0,70–0,85); spire whorls with tabulate shoulder, body whorl at



Figs 80–84. *Pseudominolia articulata* (Gould, 1861). 80–82, holotype of *Margarita articulata* Gould, 1861, diameter 7,0 mm (USNM C121); 83, 84, depressed and elevated specimens of the Natal form of the species with only two spiral cords above the periphery, Durban Bay, diameter 5,6 mm and 5,1 mm respectively (NMSA B8698).

base with much weaker, more close-set cords (lirae), very variable in number and strength, base sometimes appearing almost smooth. Axial sculpture usually weak, but some specimens from False Bay and Port Elizabeth with distinct, evenly spaced prosocline axial pliculae over virtually the entire surface (Fig. 86); pliculae cross cords rendering them somewhat granular; other specimens with at most weak subsutural pliculae and irregularly spaced growth-lines, but all with microscopic scratch-like axial lines (Figs 85, 87). Umbilicus open, of moderate width; margin roundly angular, marked by 1–2 somewhat thicker spiral cords; interior with a variable number of weak cords. Aperture roundly quadrate; outer lip prosocline, notched by spiral cords; basal lip sometimes notched at umbilical margin; columella sharply curved below parietal region.

Protoconch (Fig. 87): Typically umboniine, diameter 200–240 μm.

Colour: Immensely variable; ground colour generally white to yellowish-white, but often suffused with washes in various shades of yellow, pink, red, brown or purple; patterned with more deeply coloured spots, blotches, bands, lines, zig-zags and flames. Apex often but not invariably tinged with pink or red. Beach drift specimens from Natal and Transkei are usually more brightly coloured than material from the Cape. Dredged specimens from muddy substrata usually dull and surface of shell often partially eroded.

Dimensions: Largest specimen, diameter 8,3 mm, length 7,7 mm (fossil); largest Recent specimen, diameter 8,1 mm, length 6,6 mm.

food groove (personal observation) – a feature not present in *Pseudominolia*. *Minolia biangulosa* A. Adams, 1855, discussed by Hickman (1985), is another taxon closely related to *Pseudominolia*, but has a strongly bicarinate shell, more elaborately branched left neck lobe digits and a radula lacking even tooth base plates in the central field and with marginals bearing long slender multidenticulate cusps.

Etymology: *Pseudo-* from *pseudes* Gr., false and *Minolia* A. Adams, 1860, feminine; the false *Minolia*, referring to the historical confusion of members of this genus with *Minolia* (Solariellinae).

Key to *Pseudominolia* in southern Africa and Mozambique

1 Shell relatively large, adult diameter >10,0 mm, glossy; shoulder cord crenulate on middle spire whorls; base almost smooth ..... **splendens**
– Shell smaller, adult diameter <8,0 mm, usually rather dull; shoulder cord without crenules; base often with spiral lirae ..... **articulata**

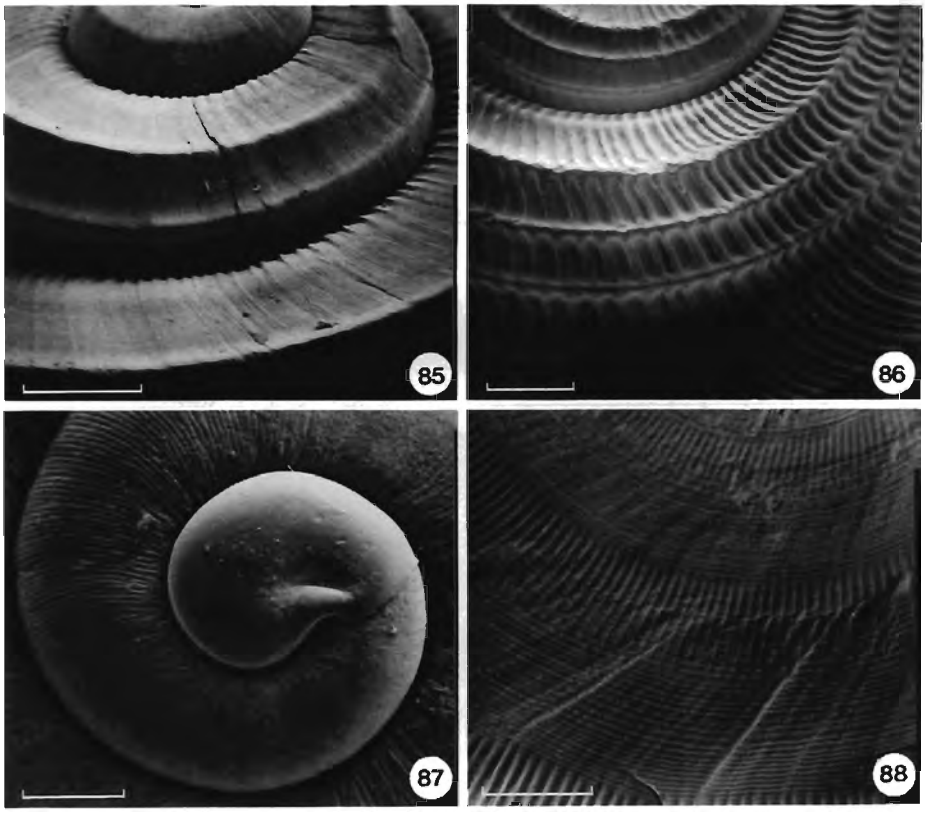
Pseudominolia articulata (Gould, 1861) **comb. n.**

Figs 78, 80–90; Map 10.

Margarita articulata Gould, 1861: 15; 1862: 153. Type loc.: Simon's Bay (in False Bay), western Cape.
Trochus (Solariella) dilectus [*non* A. Adams, 1855 = *Antisolarium egenum* (Gould, 1849)]; Sowerby, 1889: 154.
Solariella dilecta [*non* A.Adams, 1855]; Sowerby, 1892: 44, pl. 4, fig. 90 [*non Minolia dilecta*; von Martens, 1904: 15 = *Solariella bojadorensis* (Thiele, 1925)].
Gibbula articulata; Bartsch, 1915: 155, pl. 25, figs 4–6 (holotype); Turton, 1932: 184, No. 1288; Kaicher, 1986: 4602.
Solariella algoensis Thiele, 1925: 50(16), pl. 13(1), fig. 21. Type loc.: Algoa Bay (33°50,5'S:25°48,8'E), no depth given.
?Minolia bleeki Thiele, 1925: 53(19), pl. 13(1), fig. 32. Type loc.: 'Cape'.
Minolia articulata; Barnard, 1963: 233; Davies, 1972: 253; Kensley, 1973: 40, no. 86, fig. 85 [not fig. 86 = *Spectamen adarticulatum* (Barnard, 1963)].

Diagnosis: Shell lustreless, adult diameter usually <8,0 mm, elevated (L/D = 0,75–1,10); whorls corded and with a tabulate shoulder, number of cords variable; shoulder cord not crenulate, remaining obvious on body whorl; axial sculpture variable; umbilicus open, lacking callus deposit.

Description: Shell trochoid-turbiniform, height variable (L/D = 0,75–1,10); teleoconch of up to 5,5 whorls; whorls rounded but with a tabulate shoulder; suture more or less level, at or near periphery; periphery rounded, just below mid-whorl. Early whorls smooth, spiral cords developing at end of second whorl; number of cords variable; specimens from Natal usually with three cords on apical surface, one at periphery, one forming the shoulder angle and one between these; shoulder cord not crenulate; peripheral cord covered by suture and spire whorls therefore bicarinate; weaker intermediary cords may develop on body whorl; cords asymmetrically V-shaped in profile; dredged material from off Transkei generally with spire whorls tricarinate; specimens from False Bay and the western Cape represent the typical form with weaker, more numerous cords, 3–5 on spire whorls (Figs 80–82, holotype), cords more wedge-shaped in profile;



Figs 85–88. *Pseudominolia articulata* (Gould, 1861). 85, finely sculptured form, central Transkei, bar = 500 μm (NMSA C7905); 86, axially pliculate form, Port Elizabeth, bar = 500 μm (NMSA 5574); 87, protoconch, central Transkei, bar = 100 μm (NMSA C7905); 88, exterior surface of operculum showing microscopic spiral lirae, bar = 100 μm (NMSA D1972).

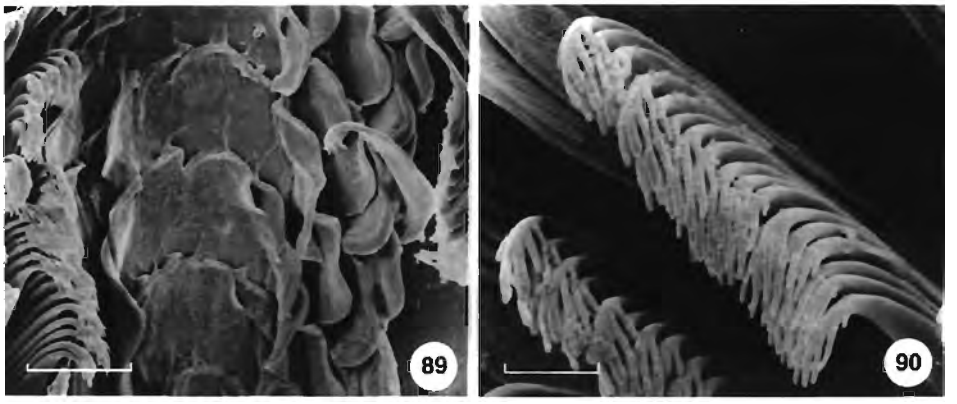
Operculum (Figs 78, 88): As in *P. splendens*, but with a broader radially striate peripheral fringe.

Radula (Figs 89–90): Thin and delicate, comprising 40–45 transverse rows; similar to that of *P. splendens*, but marginal teeth cusps dividing into longer, finger-like processes.

External anatomy: Like that of *P. splendens*; translucent white to yellowish-white, with opaque white patches; sides of foot with black pigmentation, some yellow-orange coloration on dorsal part of snout; cephalic tentacles transversely banded with black and white (alternating).

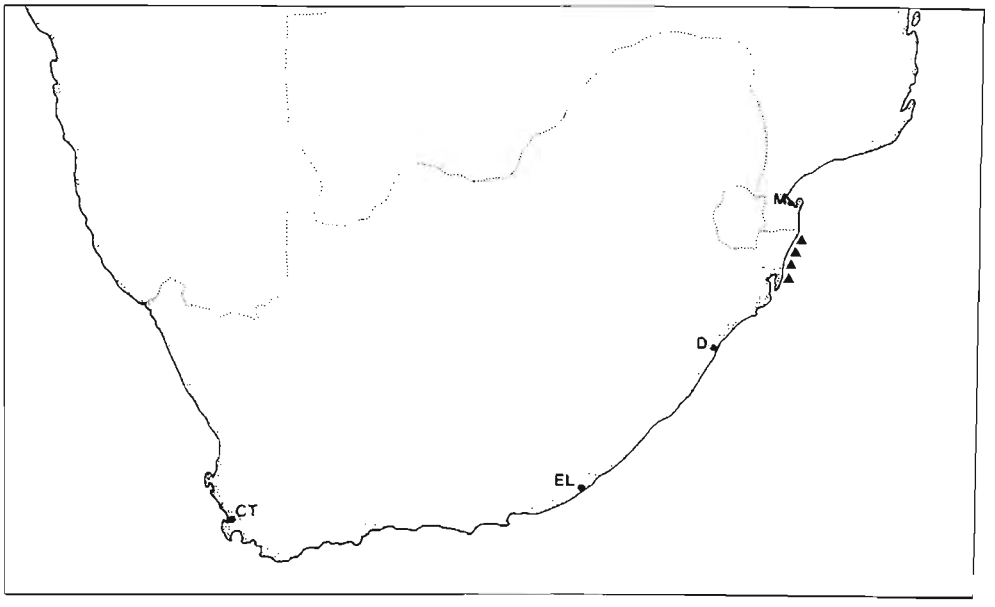
Distribution: South-western Cape (False Bay) to Natal (Durban), beach drift to 210 m, living specimens 5–140 m, often in muddy substrata.

Additional locality data (all NMSA, dredged NMDP, dead, unless indicated otherwise): NATAL: Durban Bay, shallow dredgings, B. J. Young (B8698); Salisbury Is. dredgings, B. J. Young (B2128); off Durban Bluff, sand dredged at

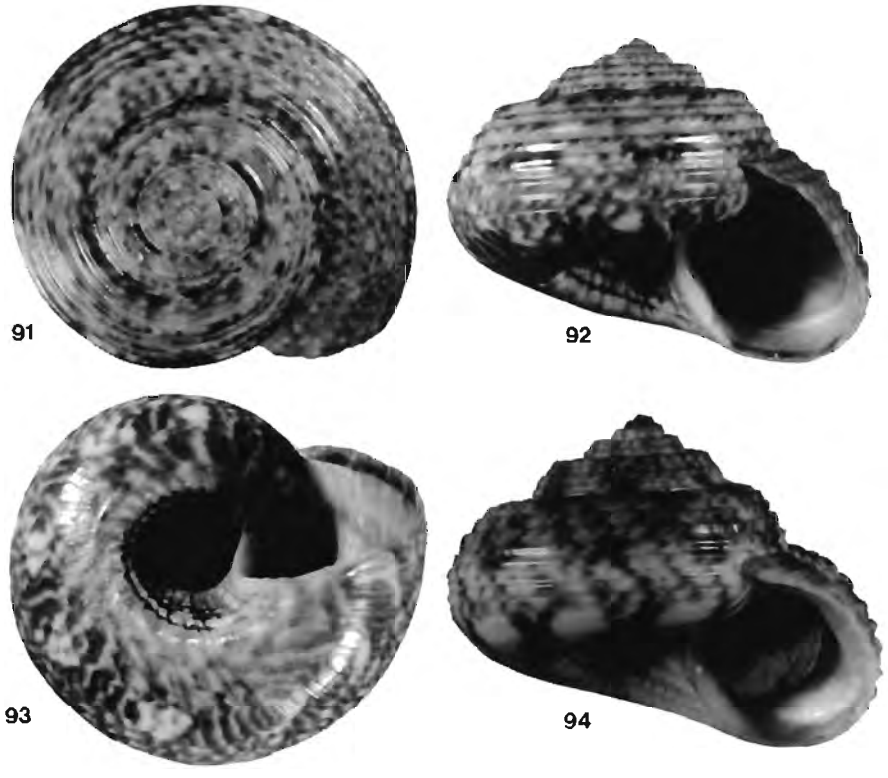


Figs 89–90. *Pseudominolia articulata* (Gould, 1861), radula (*ex* NMSA S3579); 89, central field, bar = 20 μm; 90, cusps of marginal teeth, bar = 5,0 μm.

18–22 m, N. Watt (D1659, D1657); do, 10 km, 130° S.E. of Cooper Lighthouse, 210 m, cone dredge, CSIR Water Research (A2971); Durban Bluff, H. Burnup (1236); Durban, H. Burnup, R. Kilburn (2685, B3179, 9046); Aliwal Shoal, off Umkomaas, living, 25–28 m, in sand pockets in reef, dived D. Herbert (S3345); do, Cracker Reef, *ca* 23 m, dived D. Herbert (E7140); Kelso, H. Burnup (3229); Shelly Beach, nr Port Shepstone, R. Cock, J. Marais (A3774, S3760). TRANSKEI: off Mtamvuna River, living, 120–140 m, sponge rubble (E1656);



Map 10. Southern Africa showing distribution of *Pseudominolia articulata* (Gould, 1861); each black triangle represents one or more records.



Figs 91–94. *Pseudominolia splendens* (Sowerby, 1897). 91–93, lectotype of *Solariella splendens* Sowerby, 1897, diameter 9,1 mm (BMNH 1899.4.14.3688–90); 94, lectotype of *Minolia variegata* Odhner, 1919, diameter 7,6 mm (NHRS No. 1537).

most weakly shouldered; sculpture primarily of spiral cords, shoulder cord crenulate on spire whorls, number of cords variable; base for the most part smooth; axial sculpture never strong; umbilicus open, lacking callus deposit.

Description: Shell trochoid-turbiniform, somewhat depressed (L/D = 0,70–0,85), glossy; teleoconch of up to 6,5 whorls; spire whorls with distinct tabulate shoulder, body whorl at most weakly shouldered; periphery just below mid-whorl, rounded; suture level, at periphery. Sculpture primarily of spiral cords, faint on first whorl, becoming stronger and more numerous with growth; second whorl with 2 cords, third with 2–3, the upper most of which forms the shoulder angle, fourth with 4–5; shoulder cord crenulate on spire whorls; additional cords develop on shoulder during fourth and fifth whorls and the shoulder becomes much less obvious; body whorl usually not shouldered and with *ca* 8 first order cords above and including the periphery, often with weaker intermediaries; cords wedge-shaped in profile; base with *ca* 2 weak lirae below the periphery, but remainder usually with only microscopic traces of spiral sculpture. Axial sculpture of irregularly spaced collabral growth-lines; entire surface covered by microscopic, scratch-like axial lines (Fig. 97). Umbilicus open, of moderate

width; margin slightly angled, often set off by a spiral cord, granulate in some specimens, particularly juveniles, almost smooth in others; interior of umbilicus with 1–3 cords near margin, sometimes very weak, unevenly sculptured by growth-lines. Aperture quadrate; outer lip prosocline, crenulated by cords; basal lip somewhat angled at umbilical margin; columella lip strongly angled below paries.

Protoconch: Typically umboniine, white to yellowish-white, diameter 200–220 μm.

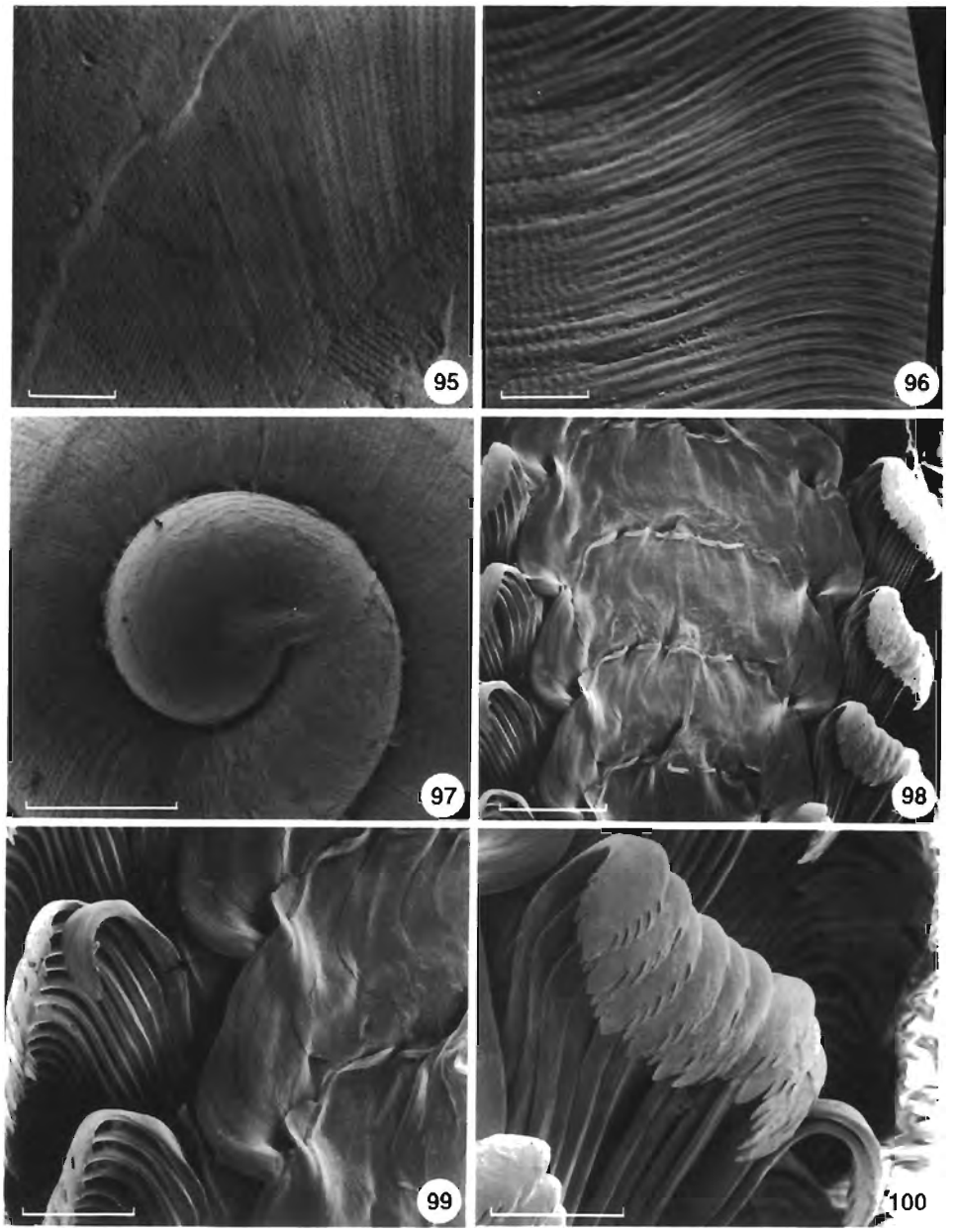
Colour: Variable; most often mottled shades of brown on apical surface; base usually with bolder markings, frequently in axial flames; sometimes with a broad spiral band of uniform colour around the umbilicus. Occasional specimens white to pink with deeper pink spiral lines; very infrequently almost entirely black.

Dimensions: Largest specimen diameter 11,8 mm, length 8,5 mm.

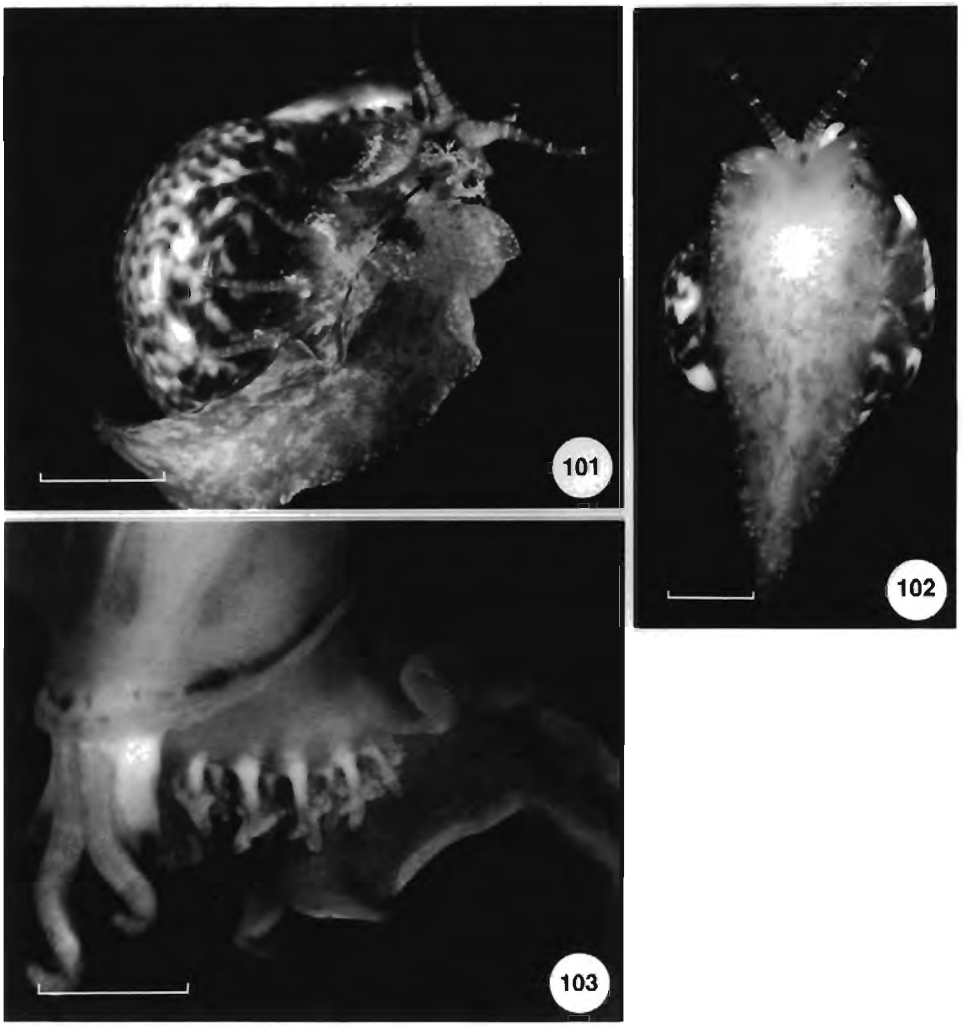
Operculum (Figs 79, 95–96): Comparatively thick, corneous; multispiral with a central nucleus, but comprising relatively few whorls; concave; external surface sculptured with fine, close-set spiral lirae; peripheral fringe moderately wide and radially striate.

Radula (Figs 98–100): Relatively short, 40–50 transverse rows; formula $\infty + (1) + 5 + 1 + 5 + (1) + \infty$; rachidian and laterals reduced to very thin, rectangular, basal plates with a slightly recurving anterior edge; no distinct shaft or cusp; outer laterals with alate basal expansion on the outer margin; overlap of basal plates extensive, but simple; marginals well developed, distal portion strongly recurved, cusp relatively short and broad (breadth more than half of length) not spatulate, and with 4–6 denticles on both margins. A latero-marginal plate (probably the innermost marginal) is present between the outermost lateral and the marginals, it retains a vestigial shaft but has no cusp.

External anatomy (Figs 77, 101–103): Body generally yellowish-white, foot often mottled with pale red-brown, white pigment spots frequent. Head lacking a distinct forehead; cephalic tentacles placed close together, almost joined basally; tentacles relatively coarsely papillate; cephalic lappets absent; eye stalks long, not fused to cephalic tentacles, eye large, terminal; no right post-optic tentacle. Snout reduced (Fig. 101), narrow and tapering, projects from beneath cephalic tentacles; snout with relatively long subterminal papillae, also with a lateral papillate ridge, papillae distally micropapillate; lips thin, gently lobed, split mid-ventrally; mouth ovate to pyriform. Left neck lobe a series *ca* 8 finger-like tentacles, anterior ones larger; each tentacle with a cluster of side branches of uneven length arising approximately half way along it (Fig. 103). Right neck lobe a broad fold, rolled to form an exhalant siphon during life; connected to base of eye stalk by a low ridge. Epipodial tentacles papillate, four on each side, arising from underside of epipodial fold, two between neck lobe and operculum, two below operculum; epipodial fold a low ridge, indented above the base of each tentacle, fold continues beyond the operculum and joins posteriorly in the mid-line; epipodial sense organs present, five on each side, one beneath neck lobe, one between first and second tentacle and one at the base of each of the three posterior tentacles. Foot truncated anteriorly, tapering to a point posteriorly;



Figs 95–100. *Pseudominolia splendens* (Sowerby, 1897). 95, 96, operculum showing microscopic spiral lirae and broad, radially striate peripheral fringe, bars = 100 μm and 50 μm respectively (NMSA D853); 97, protoconch bar = 100 μm (NMSA E1462); 98–100, radula (NMSA D853); 98, central field of radula, bar = 50 μm; 99, latero-marginal area showing cuspless latero-marginal plate (arrow), bar = 25 μm; 100, inner marginal teeth with relatively broad, multidenticulate cusps, bar = 20 μm.



Figs 101–103. *Pseudominolia splendens* (Sowerby, 1897), external anatomy; 101, living specimen emerging from upturned shell, the foot is extended just prior to the flicking self-righting mechanism, note reduced snout (arrow) projecting beneath cephalic tentacles, bar = 3,0 mm; 102, ventral view of specimen crawling on glass, note bifid propodium, bar = 3,0 mm; 103, view of anterior of left side of a relaxed, preserved specimen, note branching digits of left neck lobe, bar = 1,0 mm.

propodium indented medially and drawn out laterally into lobes (Fig. 102); sole constricted posterior to propodial lobes, but broadening to its maximum width just behind this; sides of foot not papillate.

Ctenidium monopectinate (Fig. 104), axis fused to mantle throughout its length; filaments relatively elongate with prominent bursicles and swollen tips.

Distribution: Madagascar, Mozambique, Zululand and south to the Natal

south coast; beach drift to 145 m, but usually less than 50 m (living specimens 18–50 m).

Additional locality data (all NMSA, dredged NMDP, dead, unless indicated otherwise): SOUTHERN MOZAMBIQUE: Bazaruto, west sandbank, N. Cumming (G3778). ZULULAND: off Kosi Bay, 42 m, fine sand (S3804); do, 45 m, fine muddy sand, (D6026); S.E. of Kosi River mouth, 50 m, fine sand, shell rubble, *Codium* (D7245); do, 50 m, fine muddy sand (D7789, D7868); do, 30 m, coarse sand (D7120); do, 50 m, coarse sand, shells (D6800); do, 50 m, algae, shells (E1373); do, 40 m, fine sand (D8273); do, 40 m, fine sand (D8806); do, 40 m, shell rubble (D8126); do, 48 m, sand and rubble (D8428); between Bhanga Neck and Kosi Bay, sand off outer edge of No. 13 reef, ± 34 m, dived D. Herbert *et al.* (D9764); off Rocktail Bay, 50 m, fine sand (D6425); off Hully Point, living, 35 m, few shells, algae (E815); do, living, 40 m, very fine muddy sand, algae (D8975, E1462); do, living, 30–40 m, fine muddy sand (D9008, E2900); do, living, 40 m, fine sand (D9047); do, 35–45 m, fine sand, algae, pennatulids (D9088); off Jesser Point, 50 m, fine sand (D6158, D7340); do,

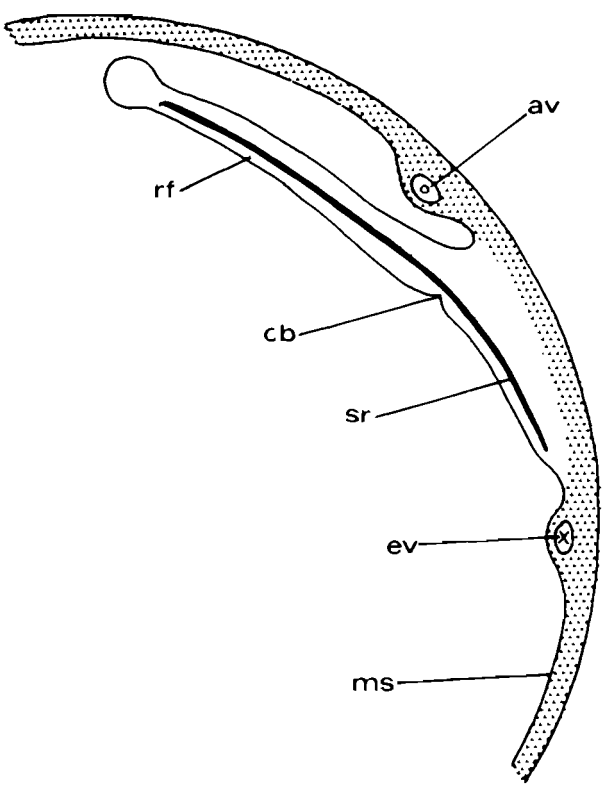
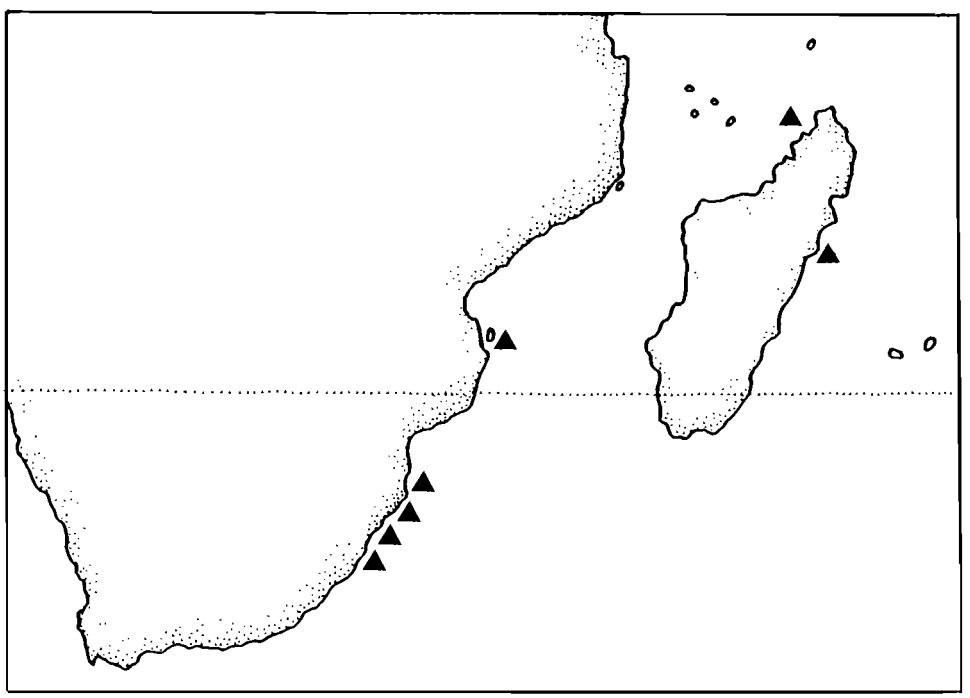


Fig. 104. *Pseudominolia splendens* (Sowerby, 1897), diagrammatic representation of a transverse section through the ctenidium and mantle skirt, in the mid to anterior portion of the ctenidium, viewed from the anterior. av, afferent ctenidial vessel; cb, ctenidial bursicle; ev, efferent ctenidial vessel; ms, mantle skirt; rf, right ctenidial filament; sr, skeletal rod supporting ctenidial filament.

48–58 m, sand, shell rubble (D6521); do, 40 m, shell rubble (D7130); do, 54 m, medium sand (D9125); do, living, 52–58 m, medium sand (D8528); off Sodwana Bay, 50 m, Smith McIntyre grab, CSIR Water Research (D2216); do, 50 m, shell grit, CSIR Water Research (A5118); do, 58 m, coral rubble (S5119); off Gipsy Hill, 47–50 m, fine sand (E3447, E3373, E4042, E4180, S1137); north of Leven Point, 32 m, dredged A. Connell (D213); N.E. of Leven Point, 42–50 m, pennatulids (E4411); off Leven Point, 50–60 m, mud (E4133, E5870); off Cape Vidal, living, 30 m, medium sand, shells (E3520); do, 75–80 m, broken shell (E4471); do, 145 m, medium sand (E4930); S.E. of Mission Rocks, 50 m, old coral rubble, *Lithothamnion* (E4639). NATAL: Off Sheffield Beach, 24 m, fine sand (E9269); do, 28 m, fine sand (E9499); 3–5 miles off Umhlanga Rocks, living, 27 m, sand and shell, dredged R. Kilburn (S1144); Durban, off south beach, 27 m, sand, dredged ORID (B4406); Durban Bay, J. Marais (S3757); Durban Bay, mangrove lagoon, R. Kilburn (8648); Durban Bay, shallow water dredgings, B. J. Young (D599, B8699); Durban Bay, Salisbury Is. dredgings, B. J. Young (B8649, B2597); Durban, H. Burnup, C. Alexander, W. Falcon (1231, 8646, 8647); Durban Bluff, H. Burnup (1232, B4166); reclaimed from Durban Bluff dredging dump, living, 18–20 m, R. Kilburn & D. Herbert (B8969); off Umlaas Canal, living, 50 m, fine sand (D971, D1021, D1049); do, living, 35–40 m, fine sand (D853, D1671); off Umkomaas, 50 m, fine sand (D3701); Shelly Beach, R. Kilburn, W. Falcon (A2036, A4578); do, J. Marais coll'n.



Map 11. South-western Indian Ocean showing distribution of *Pseudominolia splendens* (Sowerby, 1897); each black triangle represents one or more records.

Type material: Sowerby's three types of *Solariella splendens* (BMNH 1899.4.14.3688–90) remain in good condition, the largest and most typically coloured one is here figured and designated lectotype (Figs 91–93). Four syntypes of *Minolia variegata* Odhner, 1919, are present in the NHRS (invertebrate zoology coll'n No. 1537); the specimen figured by Odhner is here refigured and designated lectotype (Fig. 94).

Remarks: This species is easily recognised amongst other local umboniine species by its size, crenulated shoulder, apparent lack of axial sculpture and its overall glossy surface.

Minolia variegata Odhner, 1919, from Madagascar is a synonym. Examination of the four syntypes in the NHRS shows them to fall well within the range of variation of *splendens* and I therefore consider *variegata* to be a synonym. The types of *variegata* and the specimen recorded by Kilburn (1975) from Mozambique have a broad spiral band of uniform yellow to brown colour around the umbilicus. This is less common in specimens from the Durban area, but is also present in Zululand material. Dautzenberg (1923) mentioned both *splendens* and *variegata* from Madagascar. This was the first record of *splendens* from that area. His mention of *variegata* simply repeated Odhner's record and it seems probable that he had not seen the types of *variegata*.

Minolia variabilis A. Adams, 1853, originally of unknown locality, but subsequently recorded from the north-western Indian Ocean and China (Melvill 1928, Yen 1942), is similar and almost certainly congeneric. It differs in being more elevated, having a less well developed shoulder and in possessing spiral cords on the base. Two syntypes of *M. variabilis* are present in the BMNH (1968105), one has been figured (as the holotype) by Yen (1942). *Minolia climacota* Melvill, 1897, from the Mekran Coast is probably also congeneric.

Observations on living specimens indicate that *P. splendens* feeds by both filter-feeding and deposit-feeding. When active the snout is used to probe the surface as the animal moves along, but once every 1–2 mins the right neck lobe is lowered and appears to be wiped by the snout.

APPENDIX

The following notes and figures deal with some extralimital species examined during the course of this study.

Margarita dilecta A. Adams, 1855

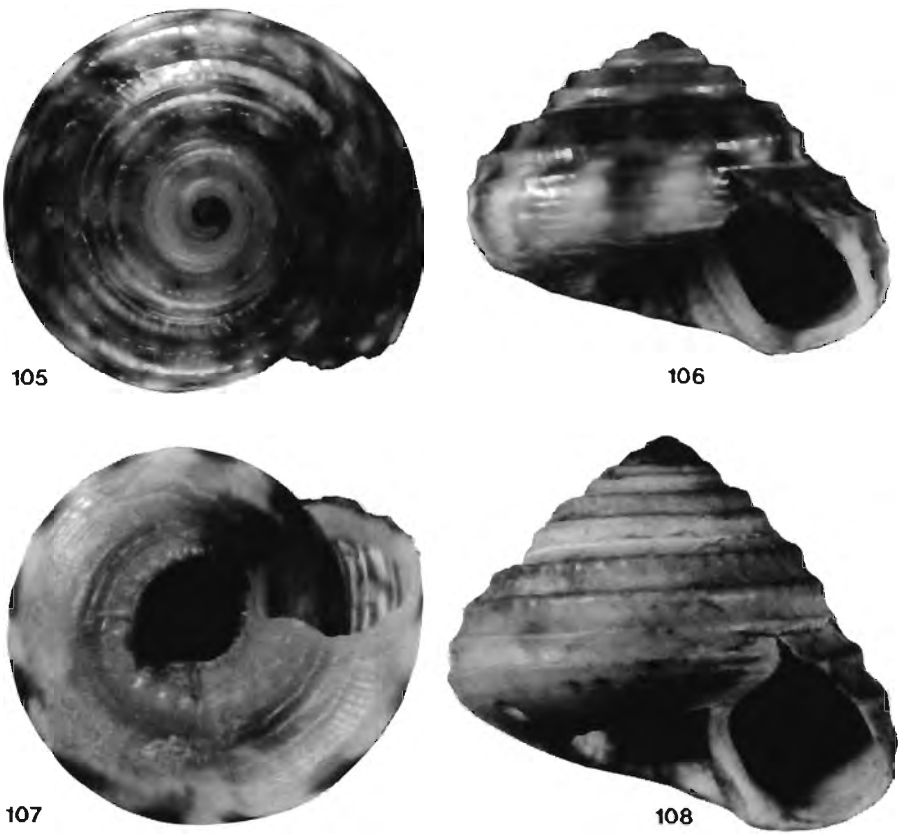
Figs 105–107

Solarium [*Torinia*] *egenum* Gould, 1849: 84; *idem*, 1852: 196, pl. 13, fig. 226 a–c. Type loc.: New Zealand.

Margarita dilecta A. Adams, 1855: 40; Pilsbry, 1889: 471; **syn. n.** Type loc.: given as 'Straits of Magellan', but evidently erroneous.

Antisolarium egenum; Finlay, 1926: 359; Powell, 1979: 65, pl.22, figs 3, 4.

This is a junior synonym of *Antisolarium egenum* (Gould, 1849). Three syntypes of *Margarita dilecta* are present in the BMNH (1968186) and these remain in good condition. One, a live-taken specimen, is here figured and



Figs 105–108. *Antisolarium egenum* (Gould, 1849). 105–107. lectotype of *Margarita dilecta* A. Adams, 1855, diameter 6,3 mm (BMNH 1968186); 108, holotype of *Solarium egenum* Gould, 1849, diameter 7,1 mm (USNM 5626).

designated lectotype (Figs 105–107). These types closely resemble *Antisolarium egenum* (Gould, 1849) from New Zealand, and although the original wood board gives the locality as 'Sts of Magellan', this has been questioned and New Zealand suggested instead. To this has been added '*egena* Gould (= *dilecta* Ad.)'. I have examined the holotype of *A. egenum* (USNM 5626)(Fig. 108) and fresh material from New Zealand (kindly provided by Bruce Marshall) and I believe this synonymy to be correct. The types of *dilecta* are not fully adult.

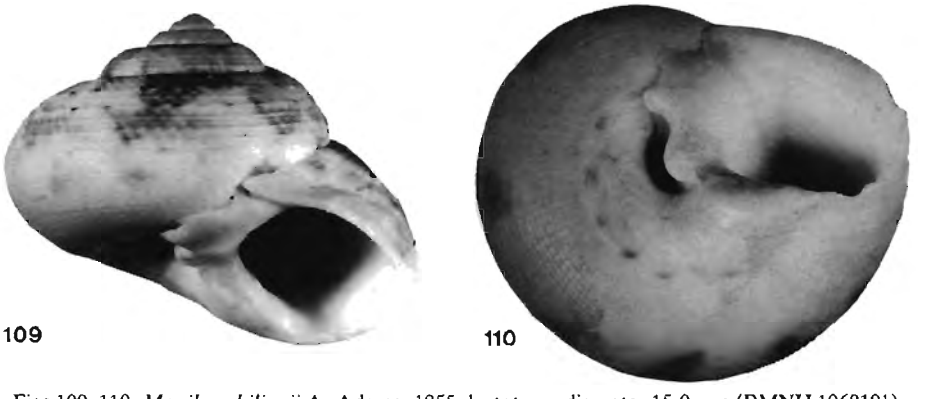
Monilea philippii A. Adams, 1855

Figs 109–110

Monilea philippii A. Adams, 1855: 39; Yen, 1942: 180, pl. 12, fig. 21. Type loc.: 'China Seas'.
Ethalia philippii; Kaicher, 1990: 5703.

Remarks: The specimen figured by Yen (1942) as the type of *Monilea philippii* is not in fact part of the type series and does not even represent the same species. It is one of a mixed lot from the China Sea (*fide* Yen) collected by Belcher (BMNH

54.5.24.173–175), erroneously identified as *M. philippii*. The type lot of *M. philippii* at the BMNH (No. 1968181) contains three specimens one of which is here figured and designated lectotype (Figs 109–110).



Figs 109–110. *Monilea philippii* A. Adams, 1855, lectotype, diameter 15,0 mm (BMNH 1968181).

The generic position of this species is not clear; the general facies of the shell and particularly the umbilical region is like that of *Ethalia*, but the thickness of the shell and its relatively coarse sculpture are reminiscent of *Monilea*. Observations on the radula and external anatomy are required.

Ethminolia impressa (G. & H. Nevill, 1869) **comb. n.**

Figs 111–116

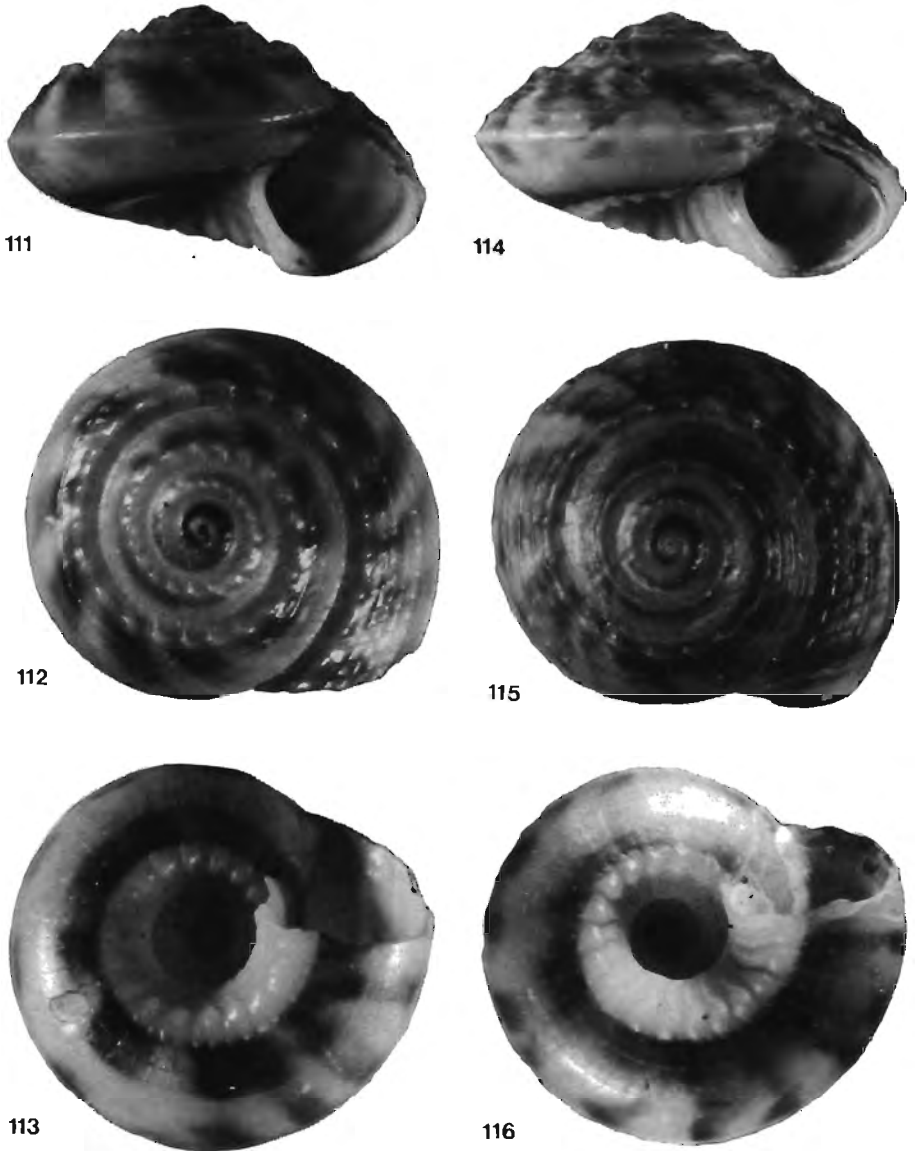
Solarium impressum G. & H. Nevill, 1869: 102, pl. 17, fig. 11, 11a; Marshall, 1887: 14, pl. 4, fig. 52; Standen & Leicester, 1906: 272; Melvill, 1928: 97 [synonym of *Minolia eudeli* (Deshayes, 1863)]; Bayer, 1940: 226; *idem*, 1948: 42. Type loc.: S. Prov. Ceylon (Sri Lanka).
Minolia eucoronata Sowerby, 1905: 187, **syn. n.** Type loc.: Ceylon.
Minolia impressa; Winckworth in Bayer, 1948: 42.

The original figures of *Solarium impressum* are very poor. Bayer (1948), at the suggestion of Winckworth, drew attention to the fact that the species was trochoidean rather than architectonicid. This had also been implied by Melvill (1928), but referral of the species to *Minolia* is clearly incorrect. The type material held in the ANSP [lots 38777 (one specimen) and 99432 (three specimens)] is all somewhat worn, but one specimen is here figured (Figs 111–113) and designated lectotype (lot 38777). Additional type material is present in the Zoological Survey of India (Subba Rao *per* Rüdiger Bieler).

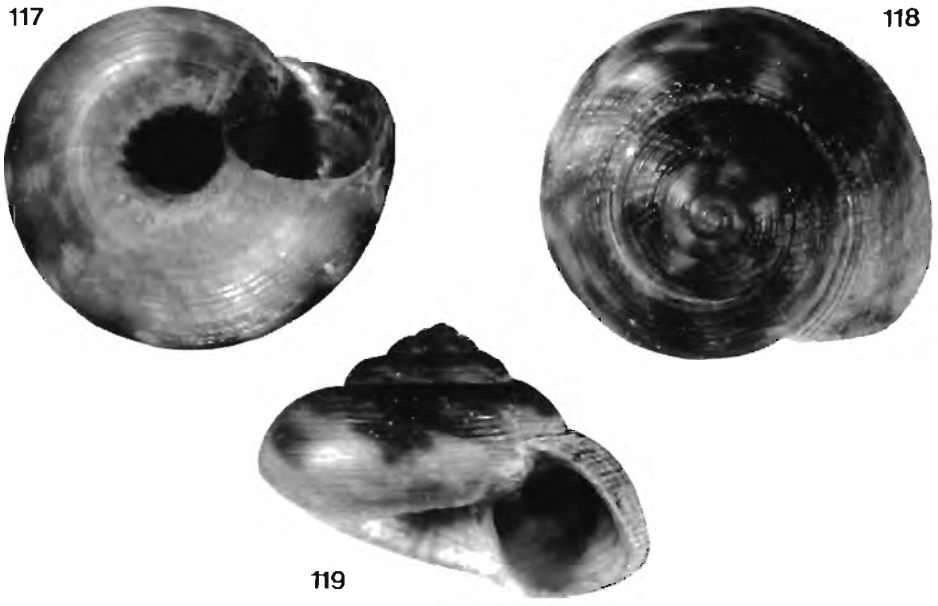
Minolia eucoronata has never been figured. Three types are present in the BMNH (1905.10.23.35–7). These are in good condition and one is here figured and designated lectotype (Figs 114–116). They are slightly larger than the types of *S. impressum*, but in other respects are very similar and there can be little doubt that only one species is involved.

The true generic affinities of this species remain to be established. On account of its similarity with *Ethminolia sculpta* (Sowerby, 1897), I have referred it to *Ethminolia*.

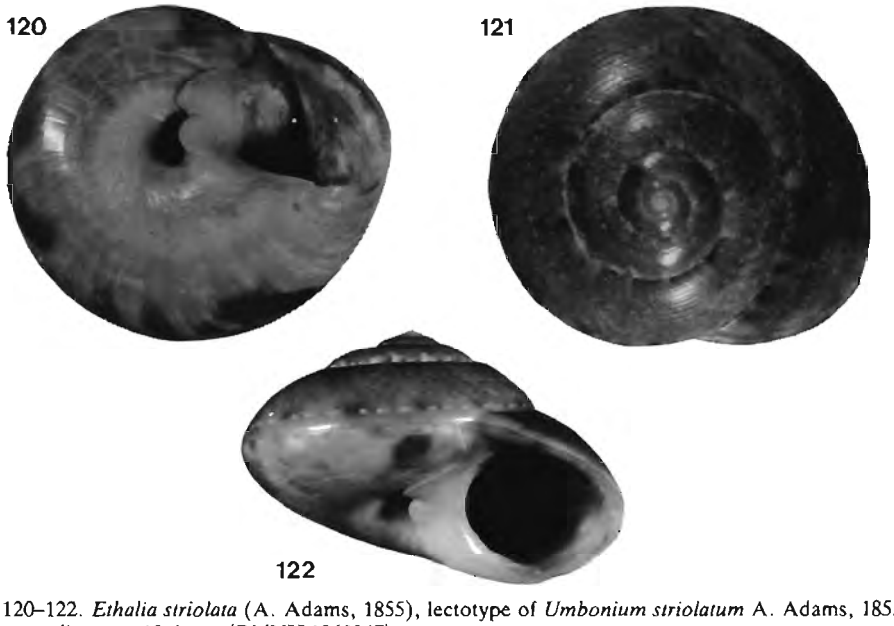
Melvill (1928) considered *Solarium impressum* to be a synonym of *Trochus eudeli* Deshayes, 1863, from Réunion Island. That species, however, differs in having a finer, more even spiral sculpture without a keel-like peripheral cord and has only fine pliculae around the umbilical margin. A syntype from the MNHN is here figured (Figs 117–119).



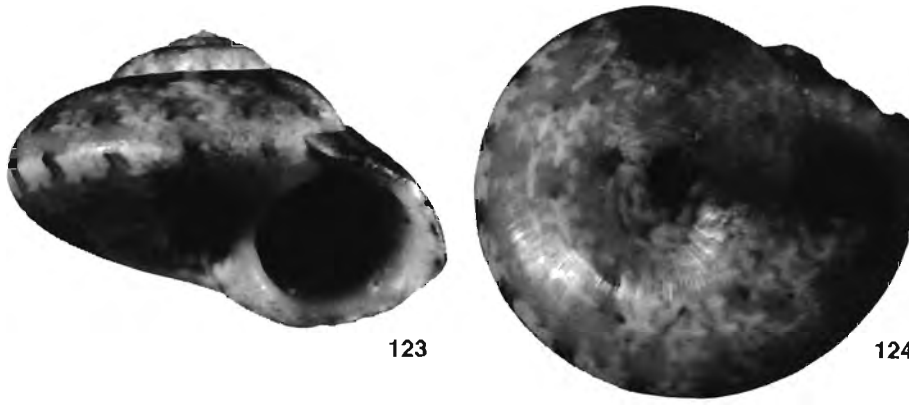
Figs 111–116. *Ethminolia impressa* (G. & H. Nevill, 1869). 111–113, lectotype of *Solarium impressum* G. & H. Nevill, 1869, diameter 4,4 mm (ANSP lot 38777); 114–116, lectotype of *Minolia eucoronata* Sowerby, 1905, diameter 5,1 mm (BMNH 1905.10.23.35–37).



Figs 117–119. *Ethminolia eudeli* (Deshayes, 1863), syntype of *Trochus eudeli* Deshayes, 1863, diameter 4,0 mm (MNHN).



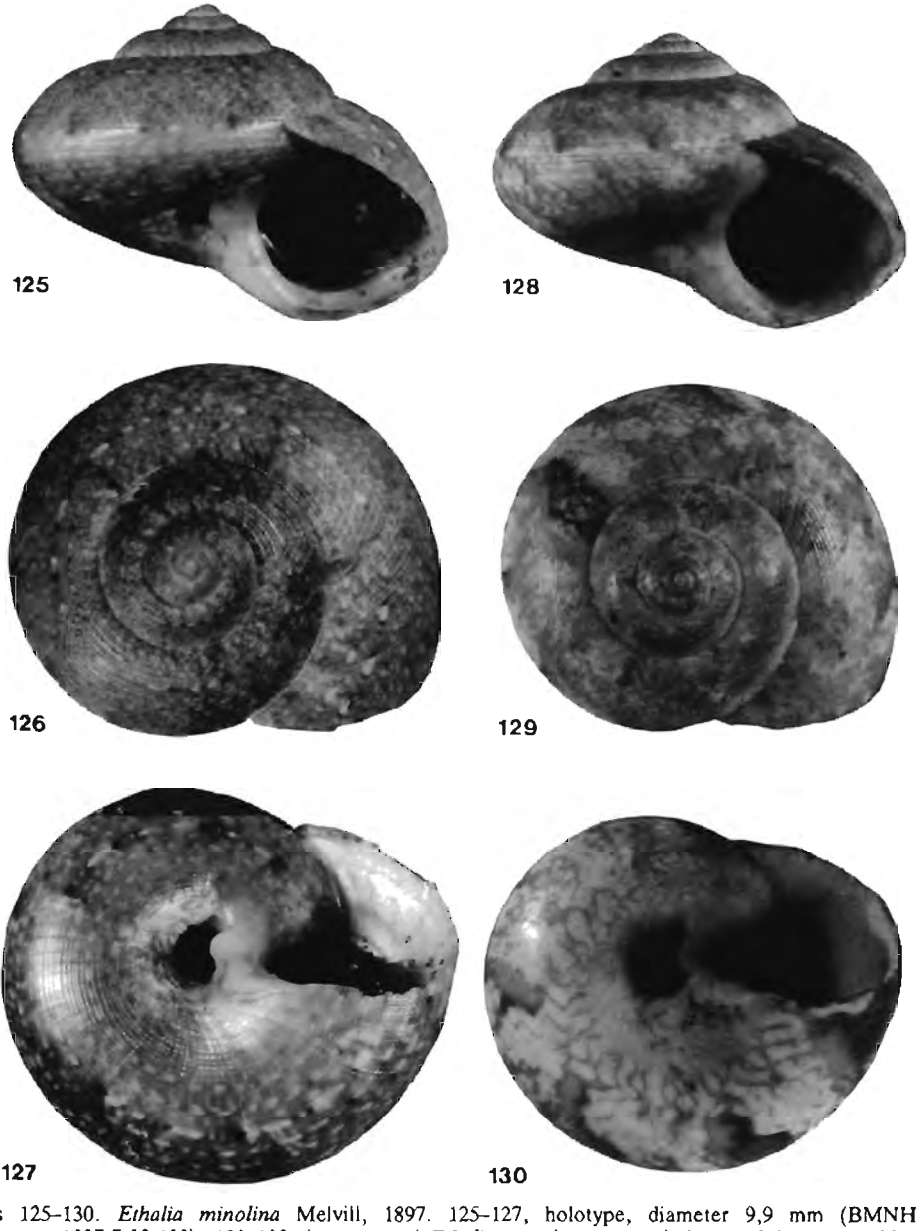
Figs 120–122. *Ethalia striolata* (A. Adams, 1855), lectotype of *Umbonium striolatum* A. Adams, 1855, diameter 12,6 mm (BMNH 1968347).



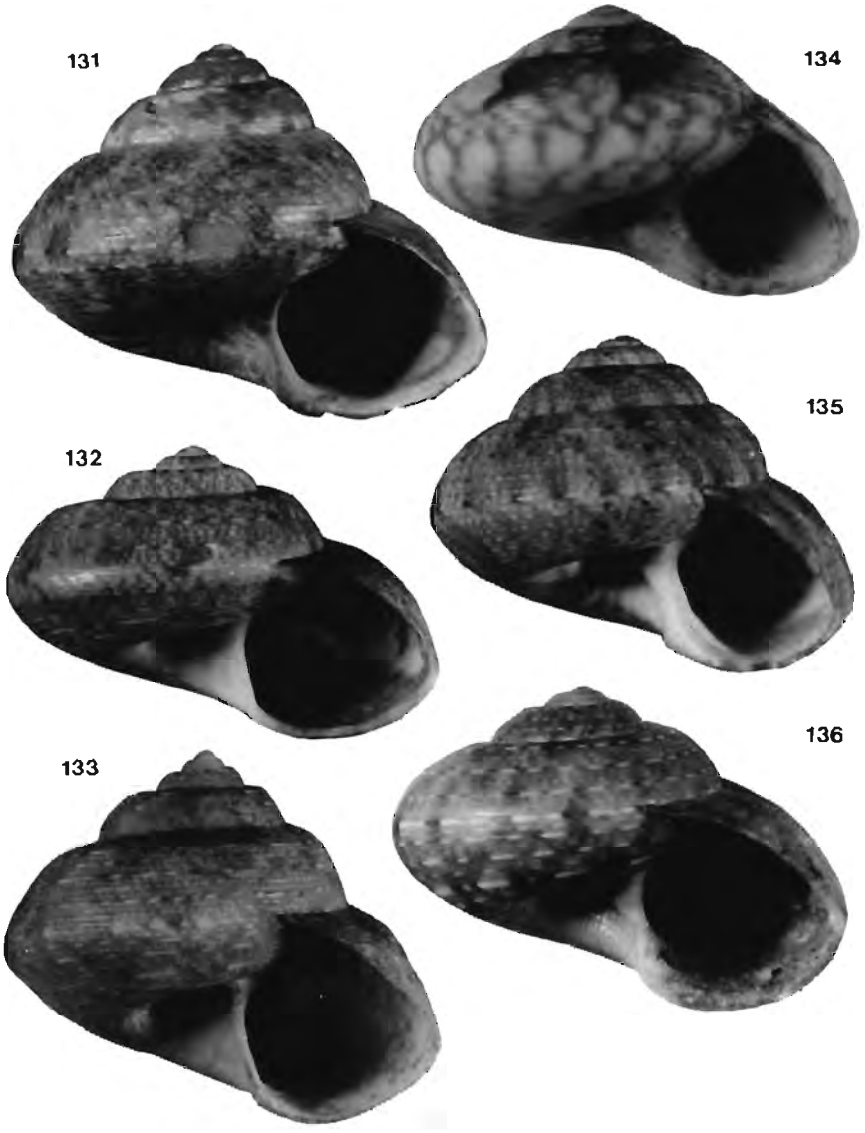
Figs 123–124. *Ethalia lamprus* (Watson, 1880), holotype of *Trochus (Solariella) lamprus* Watson, 1880, diameter, 6,1 mm (BMNH 1887.2.9.291).

ABBREVIATIONS

AMSA	Australian Museum, Sydney, Australia
ANSP	Academy of Natural Sciences, Philadelphia, USA.
BMNH	The Natural History Museum, London.
CSIR	Council for Scientific and Industrial Research, South Africa.
L/D	Length: Diameter ratio.
MCSN	Museo Civico di Storia Naturale di Genova, Italy.
MNHN	Muséum National d'Histoire Naturelle, Paris.
MVMA	Museum of Victoria, Melbourne, Australia.
NHMW	Naturhistorisches Museum, Vienna.
NHRS	Naturhistoriska Rikmusset, Stockholm.
NMSA	Natal Museum, Pietermaritzburg, South Africa.
NMDP	Natal Museum dredging programme.
NMNZ	National Museum of New Zealand, Wellington.
NMWC	National Museum of Wales, Cardiff.
NPBP	Natal Parks Board, Pietermaritzburg.
NRIO	National Research Institute for Oceanology.
ORID	Oceanographic Research Institute, Durban.
SAMA	South Australian Museum, Adelaide.
SAMC	South African Museum, Cape Town.
USNM	National Museum of Natural History, Smithsonian Institution, Washington.
ZMAN	Zoölogisch Museum, Universiteit van Amsterdam.
ZMHB	Museum für Naturkunde der Humbolt-Universität, Berlin.
ZMUC	Zoologisk Museum, København, Denmark.



Figs 125–130. *Ethalia minolina* Melvill, 1897. 125–127, holotype, diameter 9,9 mm (BMNH 1897.7.30.108); 128–130, lectotype of *Ethalia minolina* var. *infralaevior* Schepman, 1907, diameter 9,1 mm (ZMAN).



Figs 131–136. Comparative material, mostly types, examined during the course of this study. 131, *Talopena gloriola* Iredale, 1929, holotype, diameter 11,5 mm (AMSA C57737); 132, *Ethminolia vitiliginea* (Menke, 1843), diameter 10,8 mm, Victoria (NMSA J6486); 133, *Minolia eilikrines* Melvill, 1891, syntype, diameter 9,3 mm (NMWC 1955.158.128–129); 134, *Minolia edithae* Melvill, 1891, holotype, diameter 5,6 mm (NMWC 1955.158.85); 135, *Minolia glaphyrella* Melvill & Standen, 1895, lectotype, diameter 5,3 mm (NMWC 1955.158.115); 136, *Monilea vernicosa* Gould, 1861, holotype, diameter 5,3 mm (USNM 24177).

ACKNOWLEDGEMENTS

The bulk of the material discussed was dredged by the staff of the Department of Mollusca of the Natal Museum on board the research vessels *Meiring Naudé* and *Sardinops*, for the use of which we thank the National Research Institute for Oceanology and the Sea Fisheries Research Institute respectively. Thanks are extended to – R. Kilburn, B. Marshall and B. Stuckenberg for comments on the manuscript; C. Hickman and J. McLean for discussions and correspondence; the University of Natal, Pietermaritzburg for SEM facilities; the NPBP for assistance with SCUBA diving expeditions and for permission to collect material in the St Lucia and Maputaland Marine Reserves; A. Connell (CSIR Water Research), J. Marais and J. Drivas for additional specimens; L. Davis and R. Fregona (now Cook) for assistance in the preparation of illustrations. Comparative material (including types) was examined at and/or sent on loan from the following institutions: AMSA (W. Ponder and I. Loch), ANSP (G. Davis and A. Garback), BMNH (P. Mordan and K. Way), MCSN (G. Doria), MNHN (P. Bouchet), MVMA (T. Stranks), NHMW (E. Wawra via R. Janssen), NHRS (A. Warén), NMNZ (B. Marshall), NMWC (G. Oliver and A. Trew), SAMA (K. Gowlett-Holmes), SAMC (S. Ozinsky, J. Pether), USNM (M. Harasewych); ZMAN (R. G. Moolenbeek); ZMUC (T. Schiøtte); their assistance is gratefully acknowledged.

REFERENCES

ADAMS, A. 1855. Further contributions towards the natural history of the Trochidae: with the description of a new genus and of several new species, from the Cumingian collection. *Proc. zoo. Soc. Lond.* **22**(1854): 37–41.

ADAMS, H. & ADAMS, A. 1853–1854. *The genera of Recent Mollusca; arranged according to their organisation*. Vol. 1. London: John van Voorst. 484pp.

ANSELL, A. D. 1969. Escape responses of three Indian molluscs. *Veliger* **12**(2): 157–159.

BANDEL, K. 1982. Morphologie und Bildung der frühontogenetischen Gehäuse bei conchiferen Mollusken. *Facies* **7**: 1–198.

——— 1984. The radulae of Caribbean and other Mesogastropoda and Neogastropoda. *Zool. Verhand. Leiden* **214**: 1–188, pls 1–22.

BARNARD, K. H. 1963. Contributions to the knowledge of South African marine Mollusca. Part IV. Gastropoda: Prosobranchiata: Rhipidoglossa, Docoglossa. Tectibranchiata. Polyplacophora. Solenogastres. Scaphopoda. *Ann. S. Afr. Mus.* **47**(2): 201–360.

BARTSCH, P. 1915. Report on the Turton collection of South African marine mollusks with additional notes on other South African shells contained in the United States National Museum. *Bull. U.S. nat. Mus.* **91**: i–xii, 1–305, pls 1–54.

BAYER, C. 1940. Catalogue of the Solariidae in the Rijksmuseum van natuurlijke Historie. 1. *Solarium s.s. Zool. Meded. Leiden* **22**: 223–256.

——— 1948. Catalogue of the Solariidae in the Rijksmuseum van natuurlijke Historie. 3. *Torinia. Zool. Verhand. Leiden* **4**: 3–44.

BECK, L. A. 1991. *Olgaconcha tufari* n. gen. et n. sp – a new mesogastropod (Gastropoda: Prosobranchia) from hydrothermal vents in the Manus Back-Arc Basin (Bismark Sea, Papua New Guinea). *Ann. Naturhist. Mus. Wien* **92**: 277–287.

BERRY, A. J. 1984. *Umbonium vestiarium* (L.) (Gastropoda, Trochacea) as a food source for naticid gastropods and a predatory starfish on a Malaysian sandy shore. *J. moll. Stud.* **50**(1): 1–7.

——— 1986. Daily, tidal, and two-weekly spawning periodicity and brief pelagic dispersal in the tropical intertidal gastropod *Umbonium vestiarium* (L.). *J. exp. mar. Biol. Ecol.* **95**: 211–223.

DAUTZENBERG, P. 1923. Liste préliminaires des mollusques marins de Madagascar et description de deux espèces nouvelles. *J. Conchyliol., Paris* **68**(1): 21–74.

——— 1929. Contribution a l'étude de la faune de Madagascar. Mollusca II, Mollusca marina testacea. *Faunes des colonies Francais* **3**(4): 115–430 (321–636).

DAVIES, O. 1972. Pleistocene shorelines in the southern and south-eastern Cape Province (Part 2). *Ann. Natal Mus.* **21**(2): 225–279.

FINLAY, H. J. 1926. A further commentary on New Zealand molluscan systematics. *Trans. Proc. N. Z. Inst.* (1927) **57**: 320–485. Dated 1927, but offprint of paper issued in 1926 (Marshall in lit.).

FISCHER, P. 1878. Genres *Calcar*, *Trochus*, *Xenophora*, *Tectarius*, *Risella*. *In*: Kiener, L. C. *Species général et iconographie des coquilles vivantes* . . . vol. 11. Paris: J-B. Bailliere.

FRETTER, V. 1975. *Umbonium vestiarium*, a filter-feeding trochid. *J. Zool., Lond.* **177**: 541–552.

FRETTER, V. & GRAHAM, A. 1962. British prosobranch molluscs, their functional anatomy and ecology. Ray Society: London, 755pp.

——— 1977. The prosobranch molluscs of Britain and Denmark. Part 2. Trochacea. *J. moll. Stud. Suppl.* **3**: 39–100.

——— 1981. The prosobranch molluscs of Britain and Denmark. Part 6. Cerithiacea, Strombacea, Hipponicacea, Calyptraeacea, Lamellariacea, Cypraeacea, Naticacea, Tonnacea, Heteropoda. *J. moll. Stud. Suppl.* **9**: 285–363.

GLAYZER, B. A., GLAYZER, D. T. & SMYTHE, K. R. 1984. The marine Mollusca of Kuwait, Arabian Gulf. *J. Conch.* **31**(5): 311–330.

GOFAS, S., AFONSO, J. P. & BRANDÃO, M. 1986(?). *Conchas e Moluscos de Angola*. Luanda: Universidade Agostinho Neto.

GONOR, J. J. 1965. Predator-prey reactions between two marine prosobranch gastropods. *Veliger* **7**: 228–232.

GONZALEZ, E. M. L., RATO, J. A. O. & FERNANDEZ, A. V. 1983. *Fauna marina de Asturias No. 1. Moluscos. 1. Archaeogastropoda (Prosobranchia)*. Asturias: Centro de Investigaciones Acuaticas de Asturias, 75pp.

GOULD, A. A. 1849. Shells collected by the United States Exploring Expedition under the command of Charles Wilkes. *Proc. Bost. Soc. nat. Hist.* **3**: 83–85.

——— 1852. Mollusca and shells. *In* United States Exploring Expedition during the years 1839–1842 under the command of Charles Wilkes U.S.N. Vol. 12, Boston.

——— 1861. Descriptions of shells collected by the North Pacific Exploring Expedition. *Proc. Bost. Soc. nat. Hist.*. **8**: 14–40.

——— 1862. *Otia Conchologica*: descriptions of shells and mollusks from 1839 to 1862. Boston: Gould & Lincoln, iv, 256pp.

GRAHAM, A. 1938. On a ciliary process of food-collecting in the gastropod *Turritella communis* Risso. *Proc. zool. Soc. Lond.* A, **108**: 453–463.

HADFIELD, M. G. & STRATHMANN, M. F. 1990. Heterostrophic shells and pelagic development in trochoideans: implications for classification, phylogeny and palaeoecology. *J. moll. Stud.* **56**(2): 239–256.

HASZPRUNAR, G. 1988. *Sukashitrochus* sp., a scissurellid with heteropod-like locomotion (Mollusca, Archaeogastropoda). *Ann. Naturhist. Mus. Wien.* **90**(B): 367–371.

HERBERT, D. G. 1987. Revision of the Solariellinae (Mollusca: Prosobranchia: Trochidae) in southern Africa. *Ann. Natal Mus.* **28**(2): 283–382.

——— 1988. Studies on *Priotrochus obscurus* and the systematic position of *Priotrochus* (Mollusca: Gastropoda: Trochidae). *J. Zool., Lond.* **214**: 261–268.

——— 1989. *Pagodatrochus*, a new genus for *Minolia variabilis* H. Adams, 1873 (Gastropoda: Trochidae). *J. moll. Stud.* **55**(3): 365–372.

HICKMAN, C. S. 1980. Gastropod radulae and the assessment of form in evolutionary paleontology. *Paleobiology* **6**(3): 276–294.

——— 1984. Implications of radula tooth-row functional integration for archaeogastropod systematics. *Malacologia* **25**(1): 143–160.

——— 1985. Comparative morphology and ecology of free-living suspension-feeding gastropods from Hong Kong. *In*: Morton, B. & Dudgeon, D. eds, *The Malacofauna of Hong Kong and southern China II: proceedings of the second international workshop on the malacofauna of Hong Kong and southern China, Hong Kong, 1983*. Hong Kong: Hong Kong University Press.

HICKMAN, C. S. & MCLEAN, J. H. 1990. Systematic revision and suprageneric classification of trochacean gastropods. *Contributions in Science, Natural History Museum of Los Angeles County*, No. 35: 1–169.

HÖISAETER, T. 1968. Taxonomic notes on the North-European species of '*Cyclostrema*' *sensu* Jeffreys 1883 (Prosobranchia, Diotocardia). *Sarsia* **33**: 43–58.

IREDALE, T. 1924. Results from Roy Bell's molluscan collections. *Proc. Linn. Soc. New South Wales* **49**: 179–278, pls 33–36.

——— 1929. Queensland molluscan notes, I. *Mem. Queensland Mus.* **9**: 261–297.

ISCC-NBS. 1965. Color name charts illustrated with centroid colors, standard sample No 2106. Suppl. to *NBS Circular 553*, 1–4, 18 pls.

KAICHER, S. D. 1986. *Card Catalogue of world shells*. Pack No. 45, Trochidae III. St Petersburg, Florida: Kaicher.

——— 1987. *Card Catalogue of world shells*. Pack No. 50, Trochidae IV. St Petersburg, Florida: Kaicher.

——— 1990. *Card Catalogue of world shells*. Pack No. 56, Trochidae V. St Petersburg, Florida: Kaicher.

KASE, T. 1989. Autecology of *Labrocuspis*, a Middle Devonian omphalotrochid gastropod. *Lethaia* **22**(2): 149–157.

KEEN, A. M. 1960. *In*: Moore, R. C. ed. *Treatise on Invertebrate Paleontology. Part I. Mollusca* **1**. Boulder, Colorado: Geolological Society of America, i–xxiii, 1–351.

KENSLEY, B. 1973. *Sea-shells of southern Africa. Gastropods*. Cape Town: Maskew Miller for S.A. Museum, 225pp.

KILBURN, R. N. 1972. Taxonomic notes on South African marine Mollusca (2), with the description of new species and subspecies of *Conus*, *Nassarius*, *Vexillum* and *Demoulia*. *Ann. Natal Mus.* **21**(2): 391–437.

——— 1975. Taxonomic notes on South African marine Mollusca (5): including descriptions of new taxa of Rissoidae, Cerithiidae, Tonnidae, Cassididae, Buccinidae, Fasciolariidae, Turbinellidae, Turridae, Architectonicidae, Epitoniidae, Limidae and Thraciidae. *Ann. Natal Mus.* **22**(2): 577–622.

——— 1977. Taxonomic studies on the marine Mollusca of southern Africa and Mozambique. Part 1. *Ann. Natal Mus.* **23**(1): 173–214.

KILBURN, R. N. & RIPPEY, E. 1982. *Sea shells of southern Africa*. Johannesburg: Macmillan, 249pp. 46pls.

KIKUCHI, T. & DOI, T. 1987. Defensive escape response of two trochid sand snail species of the genus *Umbonium*: the effect of species-specific escape response to asteroid predators. *Publ. Amasuka mar. Biol. Lab.* **9**(1): 47–65.

KRAUSS, F. 1848. *Die südafrikanischen Mollusken. Ein Beitrag zur Kenntniss des Kap- und Natallandes und zur geographischen Verbreitung derselben, mit Beschreibung und Abbildung der neuen Arten*. Stuttgart: Ebner & Seubert i–ii, 140pp, 6pls.

KURODA, T. & HABE, T. 1952. *Checklist and bibliography of the Recent marine Mollusca of Japan*. Tokyo: Leo W. Stach.

——— 1954. New genera of Japanese marine gastropods. *Venus* **18**(2): 84–97.

KURODA, T., HABE, T. & OYAMA, K. 1971. *The sea shells of Sagami Bay*. Tokyo: Maruzen. xvi, 489pp., index.

LAMY, E. 1909*a*. Diagnoses de coquilles nouvelles recueillies par M. F. Geay à Madagascar (1905). *Bull. Mus. nat. Hist. natur.*, Paris **15**: 368–370.

——— 1909*b*. Coquilles marines recueillies par M. F. Geay à Madagascar (1905). *Mém. Soc. zool. France* **22**: 299–305, pl. 15.

LINDBERG, D. R. & DOBBERTEEN, R. A. 1981. Umbilical brood protection and sexual dimorphism in the boreal Pacific trochid gastropod, *Margarites vorticiferus* Dall. *Int. J. Invert. Reprod.* **3**: 347–355.

MAES, V. ORR. 1967. The littoral marine mollusks of Cocos-Keeling Islands (Indian Ocean). *Proc. Acad. nat. Sci. Philadelphia* **119**(4): 93–217, pls 1–26.

MARSHALL, B. A. 1988. Thysanodontinae: a new subfamily of the Trochidae (Gastropoda). *J. moll. Stud.* **54**(2): 215–229.

MARSHALL, W. B. 1887. Monograph of the Solariidae. *In*: Tryon, G. W. *Manual of Conchology*, Philadelphia: G. W. Tryon. [1]**9**: 3–32, pls 1–6.

MCLEAN, J. H. 1986. The trochid genus *Lirularia* Dall, 1909: a filter-feeder? *Am. malac. Bull.* **4**: 109.

MELVILL, J. C. 1897. Descriptions of thirty-four species of marine Mollusca from the Arabian Sea, Persian Gulf and Gulf of Oman. *Mem. Proc. Manchester lit. phil. Soc.* **41**(7): 1–26.

——— 1904. Descriptions of twelve new species and one variety of marine Gastropoda from the Persian Gulf, Gulf of Oman and Arabian Sea, collected by Mr F. W. Townsend, 1902–1904. *J. Malacol.* **11**(4): 79–85.

——— 1928. The marine Mollusca of the Persian Gulf, Gulf of Oman, and North Arabian Sea, as evidenced mainly through the collections of Captain F. W. Townsend. 1893–1914. – Addenda, corrigenda, and emendanda. *Proc. malac. Soc. Lond.* **18**: 93–117.

NEVILL, G. & NEVILL, H. 1869. Descriptions of marine Gastropoda from Ceylon, etc. *J. asiatic Soc. Bengal* **38**: 157–164.

NOMURA, S. 1940. Mollusca dredged by the *Husa-maru* from the Pacific coast of the Tiba Prefecture, Japan. *Records of oceanographic works in Japan* **12**(1): 81–116.

ODHNER, N. 1919. Contributions a la faune malacologique de Madagascar. *Ark. Zool.* **12**(6): 1–52.

OKUTANI, T. 1958. Note on shells collected off Tanegashima Island by the R. V. *Sôyô-Maru*. *Venus* **20**(2): 220–225.

——— 1961. Description of *Solariella nektonica* sp. nov. with special reference to its swimming behaviour. *Venus* **21**(3): 304–308.

OKUTANI, T. & SAKURAI, K. 1968, A new subspecies of *Solariella* from Japan Sea. *Venus* **26** (3–4): 71–73.

PILSBRY, H. A. 1889. Trochidae. *In*: Tryon, G. W. *Manual of Conchology*, Philadelphia: G. W. Tryon. [1]**11**: 1–519, pls 1–67.

——— 1895. *Catalogue of the marine mollusks of Japan, with descriptions of new species and notes on others collected by Fredrick Stearns*. Detroit, viii, 196pp, 11pls.

PONDER, W. F. 1990. A gravel beach shelled micro-gastropod assemblage from Ceuta, Strait of Gibraltar, with description of a new truncatelloidean genus. *Bull. Mus. natn. Hist. nat. Paris* **12**(A): 291–311.

POWELL, A. W. B. 1930. New species of New Zealand Mollusca from shallow-water dredgings. *Trans. Proc. N. Z. Inst.* **60**: 532–543.

——— 1979. *New Zealand Mollusca: marine, land and freshwater shells*. Auckland: Collins, xiv, 500pp.

RAMÓN, M. 1990. Spawning and development of *Calliostoma granulatum* in the Mediterranean Sea. *J. mar. biol. Ass. U.K.* **70**: 321–328.

SAVAZZI, E. & REYMENT, R. A. 1989. Subaerial hunting behaviour in *Natica gualteriana* (naticid gastropod). *Palaeogeog. Palaeoclimatol. Palaeoecol.* **74**(3–4): 355–364.

SCHEPMAN, M. M. 1908. The Prosobranchia of the *Siboga* Expedition. Part 1. Rhipidoglossa and Docoglossa; with an appendix by Prof. R. Bergh. *Siboga Expeditie, 1899–1900*. Leiden: E. J. Brill, **49**a: 1–107, pls 1–9.

SHOPLAND, E. R. 1902. List of shells collected in the neighbourhood of Aden between 1892 and 1901. *Proc. malac. Soc. Lond.* **5**: 171–179.

SMYTHE, K. R. 1982. *Seashells of the Arabian Gulf*. London: George Allen & Unwin, 123pp. 20pls.

SOWERBY, G. B. 1889. Further notes on marine shells of South Africa, with descriptions of new species. *J. Conch.* **6**(4): 147–159.

——— 1892. *Marine Shells of South Africa*. London: Sowerby, i–iv, 1–89, pls 1–5.

——— 1897. *Appendix to the Marine Shells of South Africa*. London: Sowerby, i, 1–42.

——— 1905. Descriptions of new species of marine shells, chiefly from Ceylon. *Ann. Mag. nat. Hist.* (7) **16**: 184–192.

SPRINGSTEEN, F. J. & LEOBRERA, F. M. 1986. *Shells of the Philippines*. Manila: Carfell Seashell Museum, 377pp. 100pls.

STANDEN, R. & LEICESTER, A. 1906. Report on the molluscan shells collected by Professor Herdman, at Ceylon, in 1902. *Report to the government of Ceylon on the pearl oyster fisheries of the Gulf of Manaar*. Supplementary report **38**: 267–294. London: Royal Society.

TAKI, I. 1929. Note on the soft parts of *Umbonium (Suchium) moniliferum costatum* (Kiener). *Venus* **1**: 175–179.

——— 1950. Morphological observations on the gastropod operculum. *Venus* **16**(1–4): 32–48.

THIELE, J. 1891. *In*: Troschel, F. H. *Das Gebiss der Schnecken zur Begründung einer natürlichen Classification*. Berlin. **2**(7): 251–334, pls xxv–xxviii.

——— 1924. Revision des Systems der Trochacea. *Mitt. Zool. Mus. Berlin* **11**(1): 47–74.

——— 1925. Gastropoda der Deutschen Tiefsee-Expedition 1898–1899, II. *Wiss. Ergebn. dt. Tiefsee-Exped. 'Valdivia'*. **17**(2): 35–382, pls 13–46.

——— 1929. *Handbuch der systematischen Weichtierkunde*. Jena: Fischer. **1**(1): 1–376.

TOWNSEND, F. W. 1928. Notes on shell collecting in the northern parts of the Arabian Sea, including the Gulfs of Oman and Persian Gulf in the years 1890–1914. *Proc. malac. Soc. Lond.* **18**: 118–126.

TSUCHIDA, E. & KITAO, K. 1986. On the radula and early shell of *Minolia* (Gastropoda: Prosobranchia). *Nankiseibutu* **28**(2): 85–88.

——— 1987. Studies on the molluscan fauna around Shionomisaki, southern tip of the Kii peninsula, Pacific coast of Japan – III. On the systematic position of the *'Solariella' nektonica* Okutani. *Venus* **45**(4): 258–264.

TURTON, W. H. 1932. *The marine shells of Port Alfred, South Africa*. London: Oxford University Press. xvi, 331pp, pls 1–70.

VON MARTENS, E. 1874. Ueber einige südafrikanische Mollusken. Nach der sammlung von Dr G. Fritsch. *Jb. dtsch. malak. Ges.* **1**: 119–146.

——— 1903(1904). Die beschalten Gastropoden der Deutschen Tiefsee-Expedition 1898–1899. A. Systematisch-geographischer Teil. *Wiss. Ergebn. dt. Tiefsee-Exped. 'Valdivia'*. **7**: 1–146.

WALSBY, J. & MORTON, J. 1982. *Marine molluscs. Part 1. Amphineura, Archaeogastropoda and Pulmonata*. (Cape Rodney to Okatari Point marine reserve). Auckland: University of Auckland, Leigh Marine Laboratory, i–iv, 1–89.

WARÉN, A. 1991. New and little known Mollusca from Iceland and Scandinavia. *Sarsia* **76**: 53–124.

YARON, I. 1976. *Minolia nedyma* Melvill, 1897 – an Indo-Pacific trochid in the Mediterranean. *Argamon, Israel J. Malac.* **5**(5–6): 53–60.

——— 1978. More on the generic status of *Minolia nedyma* Melvill, 1897. *Argamon, Israel J. Malac.* **6**(3–4): 27–29.

YEN, T-C. 1942. A review of Chinese gastropods in the British Museum. *Proc. malac. Soc. Lond.* **42**: 170–289.

Date received: 30 August, 1991